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HAND-BOOK

OF

PHYSIOLOGY.

KIRKES' HAND-BOOK OF PHYSIOLOGY.

HAND-BOOK
OF
PHYSIOLOGY.

BY

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ROYAL COLLEGE OF PHYSICIANS, EDINR
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PREFACE TO THE ELEVENTH EDITION.

In the preparation of the present edition of Kirkes' Physiology, we have endeavoured to maintain its character as a guide for students, especially at an early period of their career; and, while incorporating new facts and observations which are fairly established, we have as far as possible omitted the controvertible matters which should only find a place in a complete treatise or in a work of reference.

A large number of new illustrations have been added, for many of which we are indebted to the courtesy of Dr. Klein, Professor Michael Foster, Professor Schäfer, Dr. Mahomed, Mr. Gant, and Messrs. McMillan, who have been so good as to allow various figures to be copied. Our thanks are also due to Mr. Wm. Lapraik, F.C.S., who has kindly prepared a table of the absorption spectra of the blood and bile, based upon his own observations; as well as to Mr. S. K. Alcock for several careful drawings of microscopical preparations, and for reading several sheets in their passage through the press.

Mr. Danielsson, of the firm of Lebon & Co., has executed all the new figures to our entire satisfaction; and for the skill and labour he has expended upon them we are much indebted to him.

We are desirous also of acknowledging the help we have derived from the following works:—Klein's Histology;

M. Foster's Text Book of Physiology; Pavy's Food and Dietetics; Quain's Anatomy, Vol. II., Ed. ix.; Wickham Legg's Bile, Jaundice, and Bilious Diseases; Watney's Minute Anatomy of the Thymus; Rosenthal's Muscles and Nerves; Cadiat's Traité D'Anatomie Générale; Ranvier's Traité Technique D'Histologie; Landois' Lehrbuch der Physiologie des Menschen, and the Journal of Physiology.

W. MORRANT BAKER,
V. D. HARRIS.

WIMPOLE STREET,
August, 1884.

CONTENTS.

CHAPTER I.

PAGE
THE GENERAL AND DISTINCTIVE CHARACTERS OF LIVING BEINGS . . . 1

CHAPTER II.

STRUCTURAL BASIS OF THE HUMAN BODY 5
- Cells . . . . *ib.*
- Protoplasm 7
- Nucleus 11
- Intercellular Substance 20
- Fibres . . . . *ib.*
- Tubules 21

CHAPTER III.

STRUCTURE OF THE ELEMENTARY TISSUES 21
- Epithelium 22
- Connective Tissues 33
  - Areolar Tissue 37
  - White Fibrous Tissue . . . . *ib.*
  - Yellow Elastic Tissue 38
  - Gelatinous 39
  - Retiform or Adenoid 40
  - Neuroglia 41
  - Adipose 42
  - Cartilage 46
  - Bone 51
  - Teeth 67

CHAPTER IV.

THE BLOOD 78
- Quantity of Blood 79
- Coagulation of the Blood 80

M. Foster's Text Book of Physiology; Pavy's Food and Dietetics; Quain's Anatomy, Vol. II., Ed. ix.; Wickham Legg's Bile, Jaundice, and Bilious Diseases; Watney's Minute Anatomy of the Thymus; Rosenthal's Muscles and Nerves; Cadiat's Traité D'Anatomie Générale; Ranvier's Traité Technique D'Histologie; Landois' Lehrbuch der Physiologie des Menschen, and the Journal of Physiology.

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CONTENTS.

CHAPTER I.

PAGE
THE GENERAL AND DISTINCTIVE CHARACTERS OF LIVING BEINGS 1

CHAPTER II.

STRUCTURAL BASIS OF THE HUMAN BODY 5
Cells . . . . ib.
Protoplasm 7
Nucleus 11
Intercellular Substance 20
Fibres . . . . ib.
Tubules 21

CHAPTER III.

STRUCTURE OF THE ELEMENTARY TISSUES 21
Epithelium 22
Connective Tissues 33
Areolar Tissue 37
White Fibrous Tissue . . . . ib.
Yellow Elastic Tissue 38
Gelatinous 39
Retiform or Adenoid 40
Neuroglia 41
Adipose 42
Cartilage 46
Bone 51
Teeth 67

CHAPTER IV.

THE BLOOD 78
Quantity of Blood 79
Coagulation of the Blood 80

PAGE
THE BLOOD—*continued.*
Conditions affecting Coagulation 88
The Blood-Corpuscles 92
Physical and Chemical Characters of Red Blood-Cells . . . *ib.*
The White Corpuscles, or Blood-Leucocytes 98
Chemical Composition of the Blood 102
The Serum 105
Variations in Healthy Blood under Different Circumstances . . 107
Variations in the Composition of the Blood in Different Parts of the Body 108
Gases contained in the Blood 109
Blood-Crystals 112
Development of the Blood 119
Uses of the Blood 123
Uses of the various Constituents of the Blood . . . . . *ib.*

CHAPTER V.

CIRCULATION OF THE BLOOD 124
The Systemic, Pulmonary, and Portal Circulations 125
The Forces concerned in the Circulation of the Blood . . . 127

THE HEART . . . . *ib.*
Structure of the Valves of the Heart 135
The Action of the Heart 137
Function of the Valves of the Heart 139
Sounds of the Heart 145
Impulse of the Heart 147
The Cardiograph 148
Frequency and Force of the Heart's Action 151
Influence of the Nervous System on the Action of the Heart . . 154
Effects of the Heart's Action 157

THE ARTERIES, CAPILLARIES, AND VEINS 160
Structure of the Arteries 161
Structure of Capillaries 164
Structure of Veins 168
Function of the Arteries 171
The Pulse 177
Sphygmograph 178
Pressure of the Blood in the Arteries, or Arterial Tension . . 185
The Kymograph 186
Influence of the Nervous System on the Arteries 190
Circulation in the Capillaries 197
Diapedesis of Blood-Corpuscles 198

PAGE
CIRCULATION IN THE VEINS 201
Blood-pressure in the veins 202
Velocity of the Circulation 203
Velocity of the Blood in the Arteries 204
„ „ „ „ Capillaries 206
„ „ „ „ Veins . . . . ib.
Velocity of the Circulation as a whole . . . . ib.

PECULIARITIES OF THE CIRCULATION IN DIFFERENT PARTS . 208
Circulation in the Brain . . . . ib.
Circulation in the Erectile Structures 210
Agents concerned in the Circulation 211
Discovery of the Circulation 212
Proofs of the Circulation of the Blood . . . . . . ib.

CHAPTER VI.

RESPIRATION 214
Position and Structure of the Lungs 215
Structure of the Trachea and Bronchial Tubes 218
Structure of Lobules of the Lungs 221
Mechanism of Respiration 227
Respiratory Movements . . . . ib.
Respiratory Rhythm 233
Respiratory Sounds . . . . ib.
Respiratory Movements of Glottis 234
Quantity of Air respired . . . . ib.
Vital or Respiratory Capacity 235
Force exerted in Respiration 236
Circulation of Blood in the Respiratory Organs . . . . . ib.
Changes of the Air in Respiration 238
Changes produced in the Blood by Respiration 244
Mechanism of various Respiratory Actions 247
Influence of the Nervous System in Respiration 249
Effects of Vitiated Air—Ventilation 252
Effect of Respiration on the Circulation 253
Apnœa—Dyspnœa—Asphyxia 258

CHAPTER VII.

FOODS 262
Classification of Foods 264
Foods containing chiefly Nitrogenous Bodies 265
„ „ „ Carbohydrate Bodies 267

PAGE

FOODS—*continued.*
Foods containing chiefly Fatty Bodies 268
Substances supplying the Salts . . . . *ib.*
Liquid Foods . . . . *ib.*
Effects of Cooking . . . . *ib.*
Effects of an Insufficient Diet 269
Starvation 270
Effects of Improper Food 272
Effects of too much Food 273
Diet Scale 275

CHAPTER VIII.

DIGESTION 276

PASSAGE OF FOOD THROUGH THE ALIMENTARY CANAL . . . 277
Mastication 278
Insalivation 279
The Salivary Glands and the Saliva . . . . *ib.*
Structure of the Salivary Glands . . . . *ib.*
The Saliva 283
Influence of the Nervous System on the Secretion of Saliva . . 285
The Pharynx 291
The Tonsils . . . . *ib.*
The Œsophagus or Gullet 292
Swallowing or Deglutition 294

DIGESTION OF FOOD IN THE STOMACH 296
Structure of the Stomach 297
Gastric Glands 299
The Gastric Juice 303
Functions of the Gastric Juice 305
Movements of the Stomach 308
Vomiting 310
Influence of the Nervous System on Gastric Digestion . . . 312
Digestion of the Stomach after Death 313

DIGESTION IN THE INTESTINES 315
Structure of the Small Intestine . . . . *ib.*
Valvulæ Conniventes 317
Glands of the Small Intestine . . . . *ib.*
The Villi 321
Structure of the Large Intestine 325
The Pancreas and its Secretion 328

PAGE
DIGESTION IN THE INTESTINES—*continued.*
Structure of the Liver 332
Functions of the Liver 338
The Bile . . . . *ib.*
The Liver as a Blood-elaborating Organ 347
Glycogenic Function of the Liver 348
Summary of the Changes which take place in the Food during its Passage through the Small Intestine 352
Succus Entericus 351
Summary of the Process of Digestion in the Large Intestine . . 355
Defæcation 357
Gases contained in the Stomach and Intestines 358
Movements of the Intestines 359
Influence of the Nervous System on Intestinal Digestion . . 360

CHAPTER IX.

ABSORPTION 361
The Lacteal and Lymphatic Vessels and Glands . . . . . *ib.*
Lymphatic Glands 368
Properties of Lymph and Chyle 373
Absorption by the Lacteal Vessels 375
Absorption by the Lymphatic Vessels 376
Absorption by Blood-vessels 377

CHAPTER X.

ANIMAL HEAT 382
Variations in Bodily Temperature . . . . *ib.*
Sources of Heat 384
Loss of Heat 387
Production of Heat 390
Inhibitory Heat-centre 391

CHAPTER XI.

SECRETION 393
SECRETING MEMBRANES 394
SEROUS MEMBRANES . . . . *ib.*
MUCOUS MEMBRANES 396

PAGE

SECRETION—*continued.*

SECRETING GLANDS 398
PROCESS OF SECRETION 401
CIRCUMSTANCES INFLUENCING SECRETION 403
MAMMARY GLANDS AND THEIR SECRETION 405
CHEMICAL COMPOSITION OF MILK 409

CHAPTER XII.

THE SKIN AND ITS FUNCTIONS 410
Structure of the Skin . . . . *ib.*
Sudoriparous Glands 416
Sebaceous Glands 417
Structure of Hair 418
Structure of Nails 421
Functions of the Skin 422

CHAPTER XIII.

THE KIDNEYS AND URINE 422
Structure of the Kidneys 428
Structure of the Ureter and Urinary Bladder 436
The Urine 437
The Secretion of Urine 450
Micturition 460

CHAPTER XIV.

THE VASCULAR GLANDS 461
Structure and Functions of the Spleen . . . . . . *ib.*
" " " Thymus 466
" " " Thyroid 468
" " " Supra-renal capsules 469
" " " Pituitary Body 472
" " " Pineal Gland . . . . . . *ib.*
Functions of the Vascular Glands in general . . . . . *ib.*

CHAPTER XV.

CAUSES AND PHENOMENA OF MOTION 474
Ciliary Motion . . . . *ib.*
Amœboid Motion 475

PAGE
CAUSES AND PHENOMENA OF MOTION—*continued.*
Muscular Motion 476
Plain or Unstriped Muscle . . . . *ib.*
Striated Muscle 478
Development of Muscle 483
Physiology of Muscle at rest 484
„ „ in activity 488
Rigor Mortis 504
Actions of the Voluntary Muscles 507
„ „ Involuntary Muscles 511
Sources of Muscular Action 512
Electrical Currents in Nerves 513

CHAPTER XVI.

THE VOICE AND SPEECH 518
Mode of Production of the Human Voice . . . . . . *ib.*
The Larynx 520
Application of the Voice in Singing and Speaking 526
Speech 530

CHAPTER XVII.

NUTRITION: THE INCOME AND EXPENDITURE OF THE HUMAN BODY 533
Nitrogenous Equilibrium and Formation of Fat 538

CHAPTER XVIII.

THE NERVOUS SYSTEM 540
Elementary Structures of the Nervous System . . . . . *ib.*
Structure of Nerve-Fibres 541
Terminations of Nerve-Fibres 547
Structure of Nerve-Centres 550
Functions of Nerve Fibres 552
Classification of Nerve-Fibres 554
Laws of Conduction in Nerve-Fibres 555
Functions of Nerve-Centres 558
Laws of Reflex Actions 560
Secondary or Acquired Reflex Actions 562

PAGE
CEREBRO-SPINAL NERVOUS SYSTEM 564
The Spinal Cord and its Nerves 565
The White Matter of the Spinal Cord 567
The Grey Matter of the Spinal Cord 568
Nerves of the Spinal Cord 569
Functions of the Spinal Cord 573

THE MEDULLA OBLONGATA 583
Its Structure . . . . ib.
Distribution of the Fibres of the Medulla Oblongata 584
Functions of the Medulla Oblongata 587

STRUCTURE AND PHYSIOLOGY OF THE PONS VAROLII, CRURA CEREBRI, CORPORA QUADRIGEMINA, CORPORA GENICULATA, OPTIC THALAMI, AND CORPORA STRIATA 590
Pons Varolii . . . . ib.
Crura Cerebri . . . . ib.
Corpora Quadrigemina 592
Corpora Striata and Optic Thalami 593

THE CEREBELLUM 595
Functions of the Cerebellum 596

THE CEREBRUM 600
Convolutions of the Cerebrum 601
Structure of the Cerebrum 604
Chemical Composition of the Grey and White Matter 606
Functions of the Cerebrum 608
Effects of the Removal of the Cerebrum 609
Localisation of Functions 610
Experimental Localisation of Functions 613
Sleep 617

PHYSIOLOGY OF THE CRANIAL NERVES . . . . ib.
Physiology of the Third Cranial Nerve 620
" " Fourth Cranial Nerve 621
" " Fifth or Trigeminal Nerve 622
" " Sixth Nerve 627
" " Facial Nerve 628
" " Glosso-Pharyngeal Nerve 630
" " Pneumogastric Nerve 631
" " Spinal Accessory Nerve 635
" " Hypoglossal Nerve . . . . ib.

PHYSIOLOGY OF THE SPINAL NERVES 636

PHYSIOLOGY OF THE SYMPATHETIC NERVE . . . . ib.
Functions of the Sympathetic Nervous System 640

CHAPTER XIX.

PAGE
THE SENSES 646
Common Sensations . . . . ib.
Special Sensations 647

THE SENSE OF TOUCH 651

THE SENSE OF TASTE 658
The Tongue and its Papillæ 659

THE SENSE OF SMELL 666

THE SENSE OF HEARING 671
Anatomy of the Organ of Hearing 672
Physiology of Hearing 679
Functions of the External Ear . . . . ib.
Functions of the Middle Ear; the Tympanum, Ossicula, and Fenestræ 680
Functions of the Labyrinth 685
Sensibility of the Auditory Nerve 688

THE SENSE OF SIGHT 691
The Eyelids and Lachrymal Apparatus 692
The Structure of the Eye-ball . . . . ib.
Optical Apparatus 699
Accommodation of the Eye 703
Defects in the Apparatus 708
Spherical Aberration 710
Chromatic Aberration 711
The Blind Spot 713
Visual Purple 716
Colour Sensations 723
Reciprocal Action of different parts of the Retina 726
Movements of the Eye 729
Simultaneous Action of the two Eyes . . . . . . ib.

CHAPTER XX.

GENERATION AND DEVELOPMENT 736
Generative Organs of the Female . . . . ib.
Unimpregnated Ovum 739
Discharge of the Ovum 743
Menstruation 744
Corpus Luteum 747

PAGE
GENERATION AND DEVELOPMENT—*continued.*
IMPREGNATION OF THE OVUM 750
Male Sexual Functions . . . . *ib.*
Structure of the Testicle . . . . *ib.*
Spermatozoa 752
The Semen 756

DEVELOPMENT 757
Changes of the Ovum up to the Formation of the Blastoderm . *ib.*
Segmentation of the Ovum 759
Fundamental Layers of the Blastoderm: Epiblast; Mesoblast; Hypoblast 760
First Rudiments of the Embryo and its Chief Organs . . . 761
Fœtal Membranes 767
The Umbilical Vesicle 769
The Amnion and Allantois . . . . *ib.*
The Chorion 771
Changes of the Mucous Membrane of the Uterus and Formation of the Placenta 773

DEVELOPMENT OF ORGANS 778
Development of the Vertebral Column and Cranium . . . . *ib.*
„ „ Face and Visceral Arches 782
„ „ Extremities 784
„ „ Vascular System 785
Circulation of Blood in the Fœtus 796
Development of the Nervous System 798
„ „ Organs of Sense 802
„ „ Alimentary Canal 806
„ „ Respiratory Apparatus 810
„ „ Wolffian Bodies, Urinary Apparatus, and Sexual Organs 810

CHAPTER XXI.

ON THE RELATION OF LIFE TO OTHER FORCES 819

APPENDIX.

THE CHEMICAL BASIS OF THE HUMAN BODY 844

APPENDIX B:

PAGE
ANATOMICAL WEIGHTS AND MEASURES 861
Measures of Weight . . . . ib.
" " Length . . . . ib.
Sizes of various Histological Elements and Tissues 862
Specific Gravity of various Fluids and Tissues 863
Table showing the per-centage composition of various Articles of Food . . . . ib.

CLASSIFICATION OF THE ANIMAL KINGDOM 864
" " " " . . . . . . ib.

FRENCH MEASUREMENTS OF LENGTH, CAPACITY, AND WEIGHT RENDERED INTO ENGLISH EQUIVALENTS xviii
TABLE FOR CONVERTING DEGREES OF THE FAHRENHEIT THERMOMETER SCALE INTO DEGREES CENTIGRADE . . . . . ib.

INDEX 867

TO BINDER.

The Coloured Plate to face p. 115.

*Table for converting Degrees of the FAHRENHEIT Thermometer Scale into Degrees CENTIGRADE.

Fahrenheit.		Centigrade.
500°		260°
401		205
392		200
383		195
374		190
356		180
347		175
338		170
329		165
320		160
311		155
302		150
284		140
275		135
266		130
248		120
239		115
230		110
212		100
203		95
194		90
176		80
167		75
140		60
122		50
113		45
105		40·54
104		40
100		37·8
98·5		36·9
95		35
86		30
77		25
68		20
50		10
41		5
32	Zero	0
23		− 5
14		−10
+ 5		−15
− 4		−20
−13		−25
−22		−30
−40		−40
−76		−60

1 degree Fahr. = ·54° C.
1·8 ” ” = 1° C.
3·6 ” ” = 2° C.
4·5 ” ” = 2·5° C.
5·4 ” ” = 3° C.

---

* Modified from Fownes' Chemistry.

MEASUREMENTS.

FRENCH INTO ENGLISH.

LENGTH.

1 mètre, 10 décimètres, 100 centimètres, 1,000 millimètres = 39·37 English inches (or 1 yard and $3\frac{1}{3}$ in.)

1 décimètre, 10 centimètres, 100 millimètres = 3·937 inches (or nearly 4 inches)

1 centimètre, 10 millimètres = ·3937 or about (nearly $\frac{2}{5}$ inch.)

1 millimètre = nearly $\frac{1}{25}$ inch.

CAPACITY.

1,000 cubic décimètres, 1,000,000 cubic centimètres = 1 cubic metre

1 cubic décimètre or 1,000 cubic centimètres = 1 litre ($35\frac{1}{4}$ fluid oz., or rather less than an English quart)

WEIGHT.

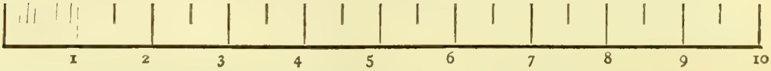
1 gramme, 10 décigrammes, 100 centigrammes, 1,000 milligrammes = 15·432349 grs. (or nearly $15\frac{1}{2}$)

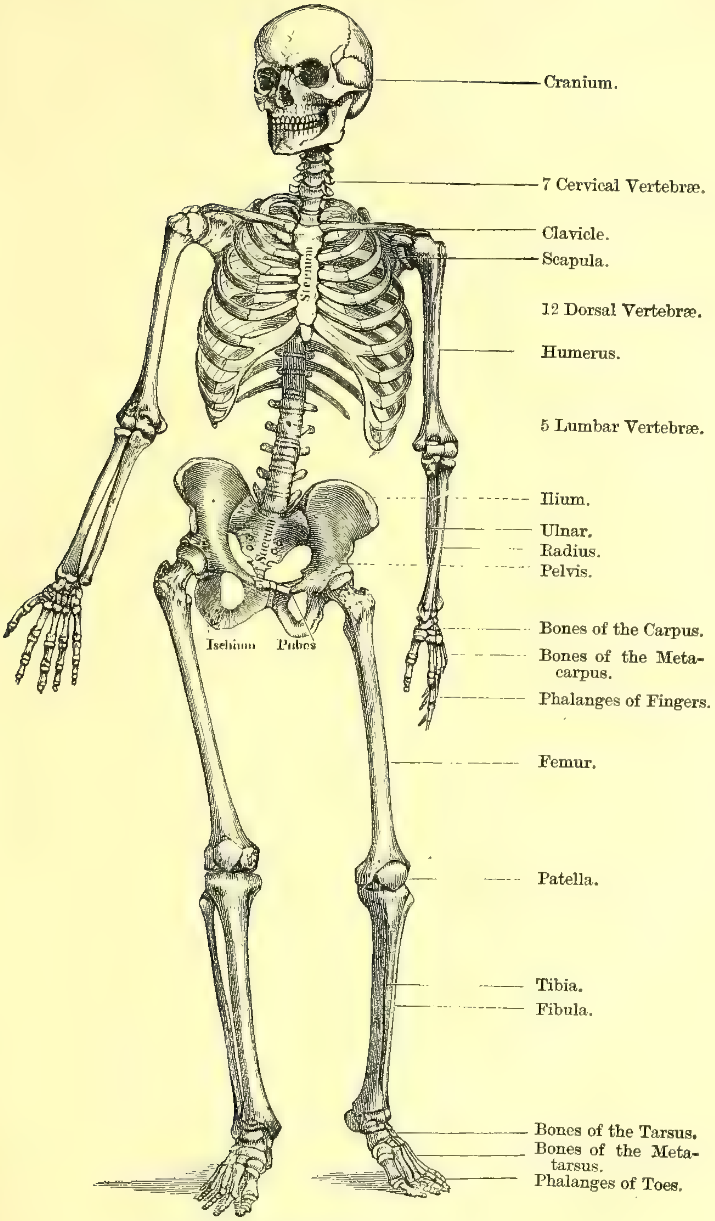
1 décigramme, 10 centigrammes, 100 milligrammes = rather more than $1\frac{1}{2}$ grain

1 centigramme, 10 décigrammes = rather more than $\frac{3}{20}$ grain

1 milligramme = rather more than $\frac{3}{200}$ grain

Measure of 1 décimètre, or 10 centimètres, or 100 millimètres.





THE SKELETON (after Holden).

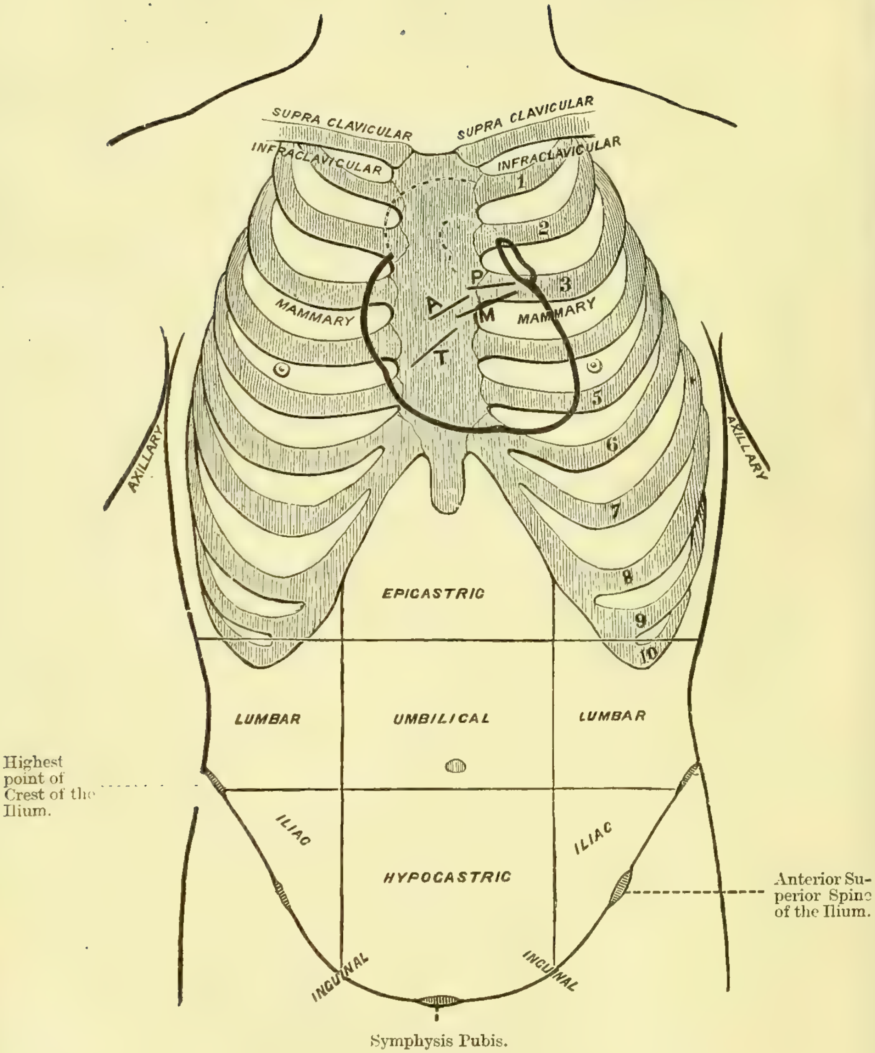


DIAGRAM OF THORACIC AND ABDOMINAL REGIONS.

A. Aortic Valve.
M. Mitral Valve.
P. Pulmonary Valve.
T. Tricuspid Valve.

HANDBOOK OF PHYSIOLOGY.

CHAPTER I.

THE GENERAL AND DISTINCTIVE CHARACTERS OF LIVING BEINGS.

HUMAN PHYSIOLOGY is the science which treats of the life of man—of the way in which he lives, and moves, and has his being. It teaches how man is begotten and born; how he attains maturity; and how he dies.

Having, then, man as the object of its study, it is unnecessary to speak here of the laws of life in general, and the means by which they are carried out, further than is requisite for the more clear understanding of those of the life of man in particular. Yet it would be impossible to understand rightly the working of a complex machine without some knowledge of its motive power in the simplest form; and it may be well to see first what are the so-called *essentials* of life—those, namely, which are manifested by all living beings alike, by the lowest vegetable and the highest animal—before proceeding to the consideration of the structure and endowments of the organs and tissue belonging to man.

The essentials of life are these,—*Birth, Growth and Development, Decline and Death.*

The term **birth**, when employed in this general sense of one of the conditions essential to life, without reference to any particular kind of living being, may be taken to mean, separation from a parent, with a greater or less power of independent life.

Taken thus, the term, although not defining any particular stage in development, serves well enough for the expression of the fact, to which no exception has yet been proved to exist, that the capacity for life in all living beings is obtained by inheritance.

Growth, or inherent power of increasing in size, although essential to our idea of life, is not confined to living beings. A crystal of common salt, or of any other similar substance, if placed under appropriate conditions for obtaining fresh material, will grow in a fashion as definitely characteristic and as easily to be foretold as that of a living creature. It is, therefore, necessary to explain the distinctions which exist in this respect between living and lifeless structures; for the manner of growth in the two cases is widely different.

Differences between Living and Lifeless Growth.—(1.) The growth of a crystal, to use the same example as before, takes place merely by additions to its outside; the new matter is laid on particle by particle, and layer by layer, and, when once laid on, it remains unchanged. The growth is here said to be *superficial*. In a living structure, on the other hand, as, for example, a brain or a muscle, where growth occurs, it is by addition of new matter, not to the surface only, but throughout every part of the mass; the growth is not superficial but *interstitial*.

(2.) All living structures are subject to constant decay; and life consists not, as once supposed, in the power of preventing this never-ceasing decay, but rather in making up for the loss attendant on it by never-ceasing repair. Thus, a man's body is not composed of exactly the same particles day after day, although to all intents he remains the same individual. Almost every part is changed by degrees; but the change is so gradual, and the renewal of that which is lost so exact, that no difference may be noticed, except at long intervals of time. A lifeless structure, as a crystal, is subject to no such laws; neither decay nor repair is a necessary condition of its existence. That which is true of structures which never had to do with life is true also with respect to those which, though they are formed by living parts, are not themselves alive. Thus, an oyster-shell is formed by the living animal which it encloses, but it is as lifeless as any other mass of inorganic matter; and in accordance with this circumstance its growth takes place, not *interstitially*, but layer by layer, and it is not subject to the constant decay and reconstruction which belong to the living. The hair and nails are examples of the same fact.

(3.) In connection with the growth of lifeless masses there is no alteration in the chemical constitution of the material which is taken up and added to the previously existing mass. For example, when a crystal of common salt grows on being placed in a fluid which contains the same material, the properties of the salt are not changed by being taken out of the liquid by the crystal and added to its surface in a solid form. But the case is essentially different in living beings, both animal and vegetable. A plant, like a crystal, can only grow when fresh material is presented to it; and this is absorbed by its leaves and roots; and animals, for the same purpose of getting new matter for growth and nutrition, take food into their stomachs. But in both these cases the materials are much altered before they are finally *assimilated* by the structures they are destined to nourish.

(4.) The growth of all living things has a definite limit, and the law which governs this limitation of increase in size is so invariable that we should be as much astonished to find an individual plant or animal without limit as to growth as without limit to life.

Development is as constant an accompaniment of life as growth. The term is used to indicate that change to which, before maturity, all living parts are constantly subject, and by which they are made more and more capable of performing their several functions. For example, a full-grown man is not merely a magnified child; his tissues and organs have not only grown, or increased in size, they have also *developed*, or become better in quality.

No very accurate limit can be drawn between the end of development and the beginning of decline; and the two processes may be often seen together in the same individual. But after a time all parts alike share in the tendency to degeneration, and this is at length succeeded by death.

Differences between Plants and Animals.—It has been already said that the essential features of life are the same in all living things; in other words, in the members of both the animal and vegetable kingdoms. It may be well to notice briefly the distinctions which exist between the members of these two kingdoms. It may seem, indeed, a strange notion that it is possible to confound vegetables with animals, but it is true with respect to the lowest of them, in which but little is manifested beyond the essentials of life, which are the same in both.

(1.) Perhaps the most essential distinction is the presence or absence of power to live upon *inorganic* material. By means of their green colouring matter, *chlorophyl*—a substance almost exclusively confined to the vegetable kingdom, plants are capable of decomposing the carbonic acid, ammonia, and water, which they absorb by their leaves and roots, and thus utilizing them as food. The result of this chemical action, which occurs only under the influence of light, is, so far as the carbonic acid is concerned, the fixation of carbon in the plant structures and the exhalation of oxygen. Animals are incapable of thus using inorganic matter, and never exhale oxygen as a product of decomposition.

The power of living upon organic as well as inorganic matter is less decisive of an animal nature; inasmuch as fungi and some other plants derive their nourishment in part from the former source.

(2.) There is, commonly, a marked difference in general chemical composition between vegetables and animals, even in their lowest forms; for while the former consist mainly of *cellulose*, a substance closely allied to starch and containing carbon, hydrogen, and oxygen only, the latter are composed in great part of the three elements just named, together with a fourth, nitrogen; the chief proximate principles formed from these being identical, or nearly so, with *albumen*. It must not be supposed, however, that either of these typical compounds alone, with its allies, is confined to one kingdom of nature. Nitrogenous compounds are freely produced in vegetable structures, although they form a very much smaller proportion of the whole organism than cellulose or starch. And while the presence of the latter in animals is much more rare than is that of the former in vegetables, there are many animals in which traces of it may be discovered, and some, the Ascidians, in which it is found in considerable quantity.

(3.) Inherent power of movement is a quality which we so commonly consider an essential indication of animal nature, that it is difficult at first to conceive it existing in any other. The capability of simple motion is now known, however, to exist in so many vegetable forms, that it can no longer be held as an essential distinction between them and animals, and ceases to be a mark by which the one can be distinguished from the other. Thus the zoospores of many of the Cryptogamia exhibit ciliary or amœboid movements (p. 9) of a like kind to those seen in animalcules; and even among the higher orders of plants, many, e.g., *Dionæa Muscipula* (Venus's fly-trap), and *Mimosa Sensitiva* (Sensitive plant), exhibit such motion, either at regular times, or on the application of external irritation, as might lead one, were this fact taken by itself, to regard them as sentient beings. Inherent power of movement, then, although especially characteristic of animal nature, is, when taken by itself, no proof of it.

(4.) The presence of a digestive canal is a very general mark by which an animal can be distinguished from a vegetable. But the lowest animals are surrounded by material that they can take as food, as a plant is surrounded by an atmosphere that it can use in like manner. And every part of their body being adapted to absorb and digest, they have no need of a special receptacle for nutrient matter, and accordingly have no digestive canal. This distinction then is not a cardinal one.

It would be tedious as well as unnecessary to enumerate the chief distinctions between the more highly developed animals and vegetables. They are sufficiently apparent. It is necessary to compare, side by side, the lowest members of the two kingdoms, in order to understand rightly how faint are the boundaries between them.

CHAPTER II.

STRUCTURAL BASIS OF THE HUMAN BODY.

By dissection, the human body can be proved to consist of various dissimilar parts, bones, muscles, brain, heart, lungs, intestines, &c., while, on more minute examination, these are found to be composed of different tissues, such as the connective, epithelial, nervous, muscular, and the like.

Cells.—Embryology teaches us that all this complex organisation has been developed from a microscopic body about $\frac{1}{120}$ in. in diameter (ovum), which consists of a spherical mass of jelly-like matter enclosing a smaller spherical body (germinal vesicle).

Further, each individual tissue can be shown largely to consist of bodies essentially similar to an ovum, though often differing from it very widely in external form. They are termed *cells:* and it must be at once evident that a correct knowledge of the nature and activities of the cell forms the very foundation of physiology.

Cells are, in fact, physiological no less than histological units.

The prime importance of the cell as an element of structure was first established by the researches of Schleiden, and his conclusions, drawn from the study of vegetable histology, were at once extended by Schwann to the animal kingdom. The earlier observers defined a cell as a more or less spherical body limited by a membrane, and containing a smaller body termed a *nucleus*, which in its turn encloses one or more *nucleoli.* Such a definition applied admirably to most vegetable cells, but the more extended investigation of animal tissues soon showed that in many cases no limiting membrane or cell-wall could be demonstrated.

The presence or absence of a cell-wall, therefore, was now regarded as quite a secondary matter, while at the same time the cell-substance came gradually to be recognised as of primary importance. Many of the lower forms of animal life, *e.g.*, the Rhizopoda, were found to consist almost entirely of matter very similar in appearance and chemical composition to the cell-substance of higher forms: and this from its chemical resemblance to flesh was termed *Sarcode* by Dujardin. When recognised in vegetable cells it was called *Protoplasm* by Mulder, while Remak applied the same name to the substance of animal cells. As the presumed formative matter in animal tissues it was termed *Blastema*, and in the belief that, wherever found, it alone of all substances has to do with generation and nutrition, Beale has named it *Germinal matter* or *Bioplasm.* Of these terms the one most in vogue at the present day is Protoplasm, and inasmuch as all life, both in the animal and vegetable kingdoms, is associated with protoplasm, we are justified in describing it, with Huxley, as the "physical basis of life."

A cell may now be defined as a nucleated mass of protoplasm,* of microscopic size, which possesses sufficient individuality to have a life-history of its own. Each cell goes through the same cycle of changes as the whole organism, though doubtless in a much shorter time. Beginning with its origin from some pre-existing cell, it grows, produces other cells, and finally dies. It is true that several lower forms of life consist of non-nucleated protoplasm, but the above definition holds good for all the higher plants and animals.

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* In the human body the cells range from the red blood-cell ($\frac{1}{3000}$ in.) to the ganglion-cell ($\frac{1}{300}$ in.).

Hence a summary of the manifestations of cell-life is really an account of the vital activities of protoplasm.

Protoplasm.—*Physical* characters.—Physically, protoplasm is viscid, varying in consistency from semi-fluid to strongly coherent. *Chemical* characters.—Chemically, living protoplasm is an extremely unstable albuminoid substance, insoluble in water. It is neutral or weakly alkaline in reaction. It undergoes heat stiffening or coagulation at about 130°F. (54·5°C.), and hence no organism can live when its own temperature is raised beyond this point, though, of course, many can exist for a time in a much hotter atmosphere, since they possess the means of regulating their own temperature. Besides the coagulation produced by heat, protoplasm is coagulated by all the reagents which produce this change in albumen. If not-living protoplasm be subjected to chemical analysis it is found to be made up of numerous bodies* besides albumen, *e.g.*, of glycogen, lecithin, salts and water, so that if living protoplasm be, as some believe, an independent chemical body, when it no longer possesses life, it undergoes a disintegration which is accompanied by the appearance of these new chemical substances. When it is examined under the microscope two varieties of protoplasm are recognised—the *hyaline*, and the *granular*. Both are alike transparent, but the former is perfectly homogeneous, while the latter (the more common variety) contains small granules or molecules of various sizes and shapes. Globules of watery fluid are also sometimes found in protoplasm; they look like clear spaces in it, and are hence called *vacuoles*.

Vital or Physiological characters.—These may be conveniently treated under the three heads of—I. **Motion**; II. **Nutrition**; and III. **Reproduction.**

I. **Motion.**—It is probable that the protoplasm of all cells is capable at some time of exhibiting movement; at any rate this phenomenon, which not long ago was regarded as quite a curiosity, has been recently observed in cells of many different kinds. It may be readily studied in the Amœbæ, in the colourless blood-cells of all vertebrata, in the branched cornea-cells of the frog, in the hairs of the stinging-nettle and Tradescantia, and the cells of Vallisneria and Chara.

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* For an account of which, reference should be made to the Appendix.

These motions may be divided into two classes—(*a*) Fluent and (*b*) Ciliary.

Another variety—the molecular or vibratory—has also been classed by some observers as vital, but it seems exceedingly probable that it is nothing more than the well-known "Brownian" molecular movement, a purely mechanical phenomenon which may be observed in any minute particles *e.g.*, of gamboge, suspended in a fluid of suitable density, such as water. Such particles are seen to oscillate rapidly to and fro, and not to progress in any definite direction.

(a.) *Fluent.*—This movement of protoplasm is rendered perceptible (1) by the motion of the granules, which are nearly always imbedded in it, and (2) by changes in the outline of its mass.

If part of a hair of Tradescantia (fig. 1) be viewed under a high magnifying power, streams of protoplasm containing crowds of granules hurrying along, like the foot passengers in a busy street, are seen flowing steadily in definite directions, some coursing round the film which lines the interior of the cell-wall, and others flowing towards or away from the irregular mass in the centre of the cell-cavity. Many of these streams of protoplasm run together into larger ones, and are lost in the central mass, and thus ceaseless variations of form are produced.

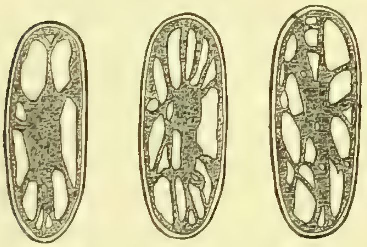


Fig. 1.—*Cell of Tradescantia* drawn at successive intervals of two minutes. The cell-contents consist of a central mass connected by many irregular processes to a peripheral film: the whole forms a vacuolated mass of protoplasm, which is continually changing its shape. (Schofield.)

In the Amœba, a minute animal consisting of a shapeless and structureless mass of sarcode, an irregular mass of protoplasm is gradually thrust out from the main body and retracted: a second mass is then protruded in another direction, and gradually the whole protoplasmic substance is, as it were, drawn into it. The Amœba thus comes to occupy a new position, and when this is repeated several times we have locomotion in a definite direction, together with a continual change of form. These movements when observed in other cells, such as the colourless blood-corpuscles of higher animals (fig. 2) are hence termed *amœboid.*

Colourless blood-corpuscles were first observed to migrate, *i.e.*, pass through the walls of the blood-vessels (p. 198), by Waller, whose observations were confirmed and extended to connective tissue corpuscles by the researches of Recklinghausen, Cohnheim, and others, and thus the phenomenon of migration has been proved to play an important part in many normal, and pathological processes, especially in that of inflammation.

This amœboid movement enables many of the lower animals to capture their prey, which they accomplish by simply flowing round and enclosing it.

The remarkable motions of pigment-granules observed in the branched pigment-cells of the frog's skin by Lister are probably due to amœboid movement. These granules are seen at one time distributed uniformly through the body and branched processes of the cell, while under the action of various stimuli (*e.g.*, light and electricity) they collect in the central mass, leaving the branches quite colourless.

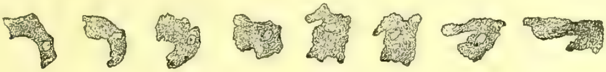


Fig. 2.—*Human colourless blood-corpuscle*, showing its successive changes of outline within ten minutes when kept moist on a warm stage. (Schofield.)

(b.) *Ciliary* action must be regarded as only a special variety of the general motion with which all protoplasm is endowed.

The grounds for this view are the following: In the case of the Infusoria, which move by the vibration of cilia (microscopic hair-like processes projecting from the surface of their bodies) it has been proved that these are simply processes of their protoplasm protruding through pores of the investing membrane, like the oars of a galley, or the head and legs of a tortoise from its shell: certain reagents cause them to be partially retracted. Moreover, in some cases cilia have been observed to develop from, and in others to be transformed into, amœboid processes.

The movements of protoplasm can be very largely modified or even suspended by external conditions, of which the following are the most important.

1. *Changes of temperature.*—Moderate heat acts as a stimulant: this is readily observed in the activity of the movements of a human colourless blood-corpuscle when placed under conditions in which its normal temperature and moisture are preserved. Extremes of heat and cold stop the motions entirely.

2. *Mechanical stimuli.*—When gently squeezed between a cover and object glass under proper conditions, a colourless blood-corpuscle is stimulated to active amœboid movement.

3. *Nerve influence.*—By stimulation of the nerves of the frog's cornea, contraction of certain of its branched cells has been produced.

4. *Chemical stimuli.*—Water generally stops amœboid movement, and by imbibition causes great swelling and finally bursting of the cells.

In some cases, however, (myxomycetes) protoplasm can be almost entirely dried up, and is yet capable of renewing its motions when again moistened.

Dilute salt-solution and many dilute acids and alkalies, stimulate the movements temporarily.

Ciliary movement is suspended in an atmosphere of hydrogen or carbonic acid, and resumed on the admission of air or oxygen.

5. *Electrical.*—Weak currents stimulate the movement, while strong currents cause the corpuscles to assume a spherical form and to become motionless.

II. **Nutrition.**—The nutrition of cells will be more appropriately described in the chapters on Secretion and Nutrition.

Before describing the Reproduction of cells it will be necessary to consider their structure more at length.

Minute Structure of Cells.—(a.) *Cell-wall.*—We have seen (p. 6) that the presence of a limiting-membrane is no essential part of the definition of a cell.

In nearly all cells the outer layer of the protoplasm attains a firmer consistency than the deeper portions: the individuality of the cell becoming more and more clearly marked as this cortical layer becomes more and more differentiated from the deeper portions of cell-substance. Side by side with this physical, there is a gradual chemical differentiation, till at length, as in the case of the fat-cells, we have a definite limiting membrane differing chemically as well as physically from the cell-contents, and remaining as a shrivelled-up bladder when they have been removed. Such a membrane is transparent and structureless, flexible, and permeable to fluids.

The cell-substance can, therefore, still be nourished by imbibition through the cell-wall. In many cases (especially in fat) a membrane of some toughness is absolutely necessary to give to the tissue the requisite consistency. When these membranes attain a certain degree of thickness and independence they are termed capsules: as examples, we may cite the capsules of cartilage-cells, and the thick, tough envelope of the ovum termed the "primitive chorion."

(b.) *Cell contents.*—In accordance with their respective ages, positions, and functions, the contents of cells are very varied.

The original protoplasmic substance may undergo many transformations; thus, in fat cells we may have oil, or fatty crystals, occupying nearly the whole cell-cavity: in pigment cells we find granules of pigment; in the various gland cells the elements of their secretions. Moreover, the original protoplasmic contents of the cell may undergo a gradual chemical change with advancing age; thus the protoplasmic cell-substance of the deeper layers of the epidermis becomes gradually converted into keratin as the cell approaches the surface. So, too, the original protoplasm of the embryonic blood-cells is replaced by the hæmoglobin of the mature coloured blood-corpuscle.

The minute structure of cells has lately been made the subject of careful investigation, and what was once regarded as homogeneous protoplasm with a few scattered granules, has been stated to be an exceedingly complex structure. In colourless blood-corpuscles, epithelial cells, connective tissue corpuscles, nerve-cells, and many other varieties of cells, an *intracellular network* of very fine fibrils, the meshes of which are occupied by a hyaline interstitial substance, has been demonstrated (Heitzmann's network) (fig. 3). At the nodes, where the fibrils cross, are little swellings, and these are the objects described as granules by the older observers: but in some cells, *e.g.*, colourless blood-corpuscles, there are real granules, which appear to be quite free and unconnected with the intra-cellular network.

(c.) *Nucleus.*—Nuclei (fig. 3) were first pointed out in the year 1833, by Robert Brown, who observed them in vegetable cells. They are either small transparent vesicular bodies containing one or more smaller particles (nucleoli), or they are semi-solid masses of protoplasm always in the resting condition bounded by a well-defined envelope. In their relation to the life of the cell they are certainly hardly second in importance to the protoplasm itself, and thus Beale is fully justified in comprising both under the term "germinal matter." They exhibit their vitality by initiating the process of division of the cell into two or more cells (fission) by first themselves dividing. Distinct observations have been made showing that spontaneous changes of form may occur in nuclei as also in nucleoli.

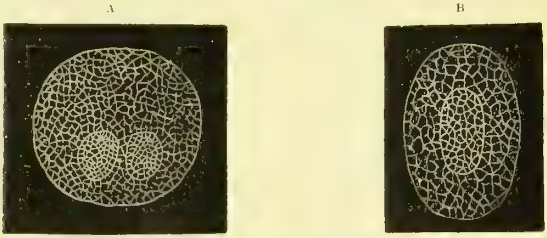


Fig. 3—(A). *Colourless blood-corpuscle showing intra-cellular network of Heitzmann*, and two nuclei with intra-nuclear network. (Klein and Noble Smith.)
(B.) *Coloured blood-corpuscle of newt showing intra-cellular network* of fibrils (Heitzmann). Also oval nucleus composed of limiting membrane and fine intra-nuclear network of fibrils. × 800. (Klein and Noble Smith.)

Histologists have long recognised nuclei by two important characters:—

(1.) Their power of resisting the action of various acids and alkalies, particularly acetic acid, by which their outline is more clearly defined, and they are rendered more easily visible. This indicates some chemical difference between the protoplasm of the cell and nuclei, as the former is destroyed by these reagents.

(2.) Their quality of staining in solutions of carmine, hæmatoxylin, &c. Nuclei are most commonly oval or round, and do not generally conform to the diverse shapes of the cells; they are altogether less variable elements than cells, even in regard to size, of which fact one may see a good example in the uniformity of the nuclei in cells so multiform as those of epithelium. But sometimes nuclei appear to occupy the whole of the cell, as is the case in the lymph corpuscles of lymphatic glands and in some small nerve cells.

Their position in the cell is very variable. In many cells, especially where active growth is progressing, two or more nuclei are present.

The nuclei of many cells have been shown to contain a fine *intra-nuclear network* in every respect similar to that described above as intra-cellular (fig. 3), the interstices of which are occupied by semi-fluid protoplasm.

III. **Reproduction.**—The life of individual cells is probably very short in comparison with that of the organism they compose: and their constant decay and death necessitate constant reproduction. The mode in which this takes place has long been the subject of great controversy.

In the case of plants, all of whose tissues are either cellular or composed of cells which are modified or have coalesced in various ways, the theory that all new cells are derived from pre-existing ones was early advanced and very generally accepted. But in the case of animal tissues Schwann and others maintained a theory of spontaneous or free cell formation.

According to this view a minute corpuscle (the future nucleolus) springs up spontaneously in a structureless substance (blastema) very much as a crystal is formed in a solution. This nucleolus attracts the surrounding molecules of matter to form the nucleus, and by a repetition of the process the substance and wall are produced.

This theory, once almost universally current, was first disputed and finally overthrown by Remak and Virchow, whose researches established the truth expressed in the words "Omnis cellula e cellulâ."

It will be seen that this view is in strict accordance with the truth established much earlier in Vegetable Histology that every cell is descended from some pre-existing (mother-) cell. This derivation of cells from cells takes place by (1) *gemmation*, or (2) *fission* or *division*.

(1.) *Gemmation.*—This method has not been observed in the human body or the higher animals, and therefore requires but a passing notice. It consists essentially in the budding off and separating of a portion of the parent cell.

(2.) *Fission* or *Division.*—As examples of reproduction by fission, we may select the ovum, the blood cell, and cartilage cells.

In the frog's ovum (in which the process can be most readily observed) after fertilization has taken place, there is first some amœboid movement, the oscillation gradually increasing until a permanent dimple appears, which gradually extends into a furrow running completely round the spherical ovum, and deepening until the entire yelk-mass is divided into two hemispheres of protoplasm each containing a nucleus (fig. 4, *b*). This process being repeated by the formation of a second furrow at right angles to the first, we have four cells produced (*c*): this subdivision is carried on till the ovum has been divided by segmentation into a mass of cells (mulberry-mass) (*d*) out of which the embryo is developed.

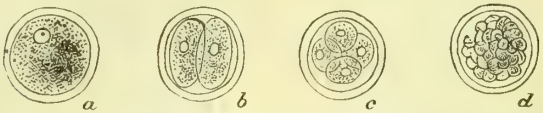


Fig. 4.—*Diagram of an ovum* (*a*) *undergoing segmentation.* In (*b*) it has divided into two; in (*c*) into four; and in (*d*) the process has ended in the production of the so-called "mulberry mass." (Frey.)

Segmentation is the first step in the development of most animals, and doubtless takes place in man.

Multiplication by fission has been observed in the colourless blood-cells of many animals. In some cases (fig. 5), the process has been seen to commence with the nucleolus which divides within the nucleus. The nucleus then elongates, and soon a well-marked constriction occurs, rendering it hour-glass shaped, till finally it is separated into two parts, which gradually recede from each other: the same process is repeated in the cell-substance, and at length we have two cells produced which by rapid growth soon attain the size of the parent cell (*direct division*). In some cases there is a primary fission into three instead of the usual two cells.

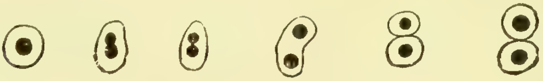


Fig. 5.—*Blood-corpuscle from a young deer embryo,* multiplying by fission. (Frey.)

In cartilage (fig. 6), a process essentially similar occurs, with the exception that (as in the ovum) the cells produced by fission remain in the original capsule, and in their turn undergo division, so that a large number of cells are sometimes observed within a common envelope. This process of fission within a capsule has been by some described as a separate method, under the title "endogenous fission," but there seems to be no sufficient reason for drawing such a distinction.

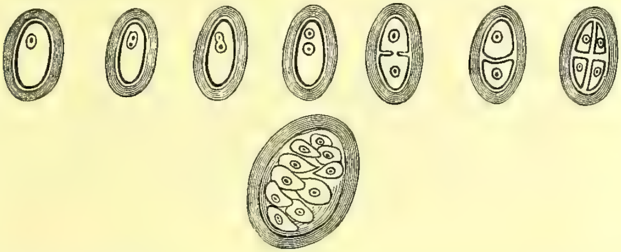


Fig. 6.—*Diagram of a cartilage cell undergoing fission within its capsule.* The process of division is represented as commencing in the nucleolus, extending to the nucleus, and at length involving the body of the cell. (Frey.)

It is important to observe that fission is often accomplished with great rapidity, the whole process occupying but a few minutes, hence the comparative rarity with which cells are seen in the act of dividing.

Indirect cell division.—In certain and numerous cases the division of cells does not take place by the simple constriction of their nuclei and surrounding protoplasm into two parts as above described (direct division), but is preceded by complicated changes in their nuclei (karyokinesis). These changes consist in a gradual rearrangement of the intranuclear network of each nucleus, until two nuclei are formed similar in all respects to the original one. The nucleus in a resting condition, *i.e.*, before any changes preceding division occur, consists of a very close meshwork of fibrils, which stain deeply in carmine, imbedded in protoplasm, which does not possess this property, the whole nucleus being contained in an envelope. The first change consists of a slight enlargement, the disappearance of the envelope, and the increased definition and thickness of the nuclear fibrils, which are also more separated than they were and stain better. This is the stage of *con-*

volution (fig. 7, B, C). The next step in the process is the arrangement of the fibrils into some definite figure by an alternate looping in and out around a central space, by which means the *rosette* or *wreath* stage (fig. 7, D) is reached. The loops of the rosette next become divided at the periphery, and their central points become more angular, so that the fibrils, divided into portions of about equal length, are, as it were, doubled at an acute angle, and radiate V-shaped from the centre, forming a *star* (aster) or wheel (fig. 7, E), or perhaps from two centres, in which case a double star (diaster) results (fig. 7, G, H, and I). After remaining almost unchanged for some time, the V-shaped fibres being first re-arranged in the centre, side by side (angle outwards), tend to separate into two bundles, which gradually assume position at either pole. From these groups of fibrils the two nuclei of the new cells are formed (daughter nuclei) (fig. 7, K), and the changes they pass through before reaching the resting condition are exactly those through which the original nucleus (mother nucleus) has gone, but in a reverse order, viz., the star, the rosette, and the convolution. During or shortly after the formation of the daughter nuclei the cell itself becomes constricted, and then divides in a line about midway between them.

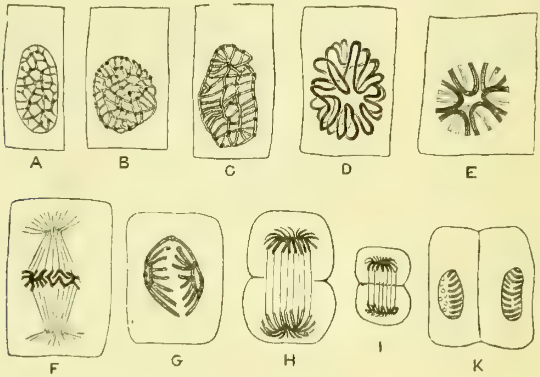


Fig. 7.—*Karyokinesis.* A, ordinary nucleus of a columnar epithelial cell; B, C, the same nucleus in the stage of *convolution;* D, the *wreath or rosette* form; E, the *aster* or single star; F, a nuclear spindle from the Descemet's endothelium of the frog's cornea; G, H, I, diaster; K, two daughter nuclei. (Klein.)

Functions of Cells.—The functions of cells are almost infinitely varied and make up nearly the whole of Physiology. They will be more appropriately considered in the chapters treating of the several organs and systems of organs which the cells compose.

Decay and Death of Cells.—There are two chief ways in which the comparatively brief existence of cells is brought to an end. (1) Mechanical abrasion, (2) Chemical transformation.

1. The various epithelia furnish abundant examples of mechanical abrasion. As it approaches the free surface the cell becomes more and more flattened and scaly in form and more horny in consistence, till at length it is simply rubbed off. Hence we find epithelial cells in the mucus of the mouth, intestine, and genito-urinary tract.

2. In the case of chemical transformation the cell-contents undergo a degeneration which, though it may be pathological, is very often a normal process.

Thus we have (a.) *fatty* metamorphosis producing oil-globules in the secretion of milk, fatty degeneration of the muscular fibres of the uterus after the birth of the fœtus, and of the cells of the Graafian follicle giving rise to the "corpus luteum." (See chapter on Generation.)

(b.) *Pigmentary* degeneration from deposit of pigment, as in the epithelium of the air-vesicles of the lungs.

(c.) *Calcareous* degeneration which is common in the cells of many cartilages.

Having thus reviewed the life-history of cells in general, we may now discuss the leading varieties of form which they present.

In passing, it may be well to point out the main *distinctions between animal and vegetable cells.*

It has been already mentioned that in animal cells an envelope or cell-wall is by no means always present. In adult vegetable cells, on the other hand, a well-defined cellulose wall is highly characteristic; this, it should be observed, is non-nitrogenous, and thus differs chemically as well as structurally from the contained mass.

Moreover, in vegetable cells (fig. 8, B), the protoplastic contents of the cell fall into two subdivisions: (1) a continuous film which lines the interior of the cellulose wall; and (2) a reticulate mass containing the nucleus and occupying the cell-cavity; its interstices are filled with fluid. In young vegetable cells such a distinction does not exist; a finely granular protoplasm occupies the whole cell-cavity (fig. 8, A).

Another striking difference is the frequent presence of a large quantity of intercellular substance in animal tissues, while in vegetables it is comparatively rare, the requisite consistency being given to their tissues by the tough cellulose walls, often thickened by deposits of lignin. In animal cells this end is attained by the deposition of lime-salts in a matrix of intercellular substance, as in the process of ossification.

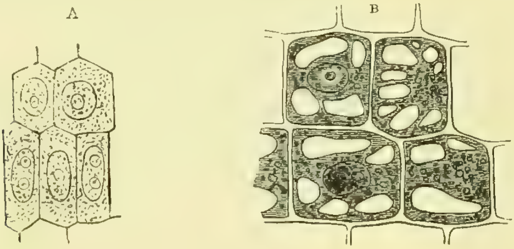


Fig. 8.—(A). *Young vegetable cells*, showing cell-cavity entirely filled with granular protoplasm enclosing a large oval nucleus, with one or more nucleoli.
(B.) *Older cells* from same plant, showing distinct cellulose-wall and vacuolation of protoplasm.

Forms of Cells.—Starting with the spherical or spheroidal (fig. 9, *a*) as the typical form assumed by a free cell, we find this altered to a polyhedral shape when the pressure on the cells in all directions is nearly the same (fig. 9, *b*).

Of this, the primitive segmentation-cells may afford an example.

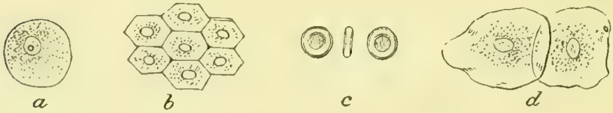


Fig. 9.—*Various forms of cells.* *a.* Spheroidal, showing nucleus and nucleolus. *b.* Polyhedral. *c.* Discoidal (blood-cells). *d.* Scaly or squamous (epithelial cells).

The discoid shape is seen in blood-cells (fig. 9, *c*), and the scale-like form in superficial epithelial cells (fig. 9, *d*). Some cells have a jagged outline (prickle-cells) (fig. 13).

Cylindrical, conical, or prismatic cells occur in the deeper layers of laminated epithelium, and the simple cylindrical epithelium of the intestine and many gland ducts. Such cells may taper off at one or both ends into fine processes, in the former case being caudate, in the latter fusiform (fig. 10). They may be greatly elongated so as to become fibres. Ciliated cells (fig. 10, *d*) must be noticed as a distinct variety: they possess, but only on their free surfaces, hair-like processes (cilia). These vary immensely in size, and may even exceed in length the cell itself. Finally we have the branched or stellate cells, of which the large nerve-cells of the spinal cord, and the connective tissue corpuscle are typical examples (fig. 10, *e*). In these cells the primitive branches by secondary branching may give rise to an intricate network of processes.

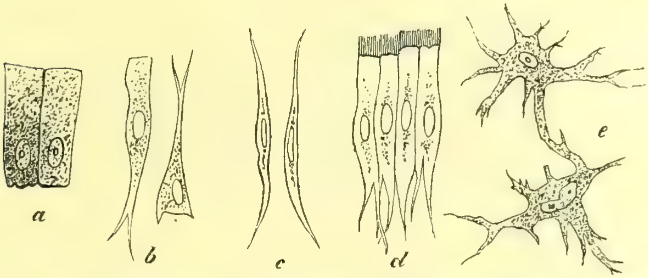


Fig. 10.—*Various forms of cells.* *a.* Cylindrical or columnar. *b.* Caudate. *c.* Fusiform. *d.* Ciliated (from trachea). *e.* Branched, stellate.

Classification of Cells.—Cells may be classified in many ways. According to :—

(a.) *Form :* They may be classified into spheroidal or polyhedral, discoidal, flat or scaly, cylindrical, caudate, fusiform, ciliated and stellate.

(b.) *Situation :*—we may divide them into blood cells, gland cells, connective tissue cells, &c.

(c.) *Contents :*—fat and pigment cells and the like.

(d.) *Function :*—secreting, protective, contractile, &c.

(e.) *Origin :*—hypoblastic, mesoblastic, and epiblastic cells. (See chapter on Generation.)

It remains only to consider the various ways in which cells are connected together to form tissues, and the transformations by which intercellular substance, fibres and tubules are produced.

Modes of connection.—Cells are connected :—

(1) By a cementing intercellular substance. This is probably always present as a transparent, colourless, viscid, albuminous

substance, even between the closely apposed cells of cylindrical epithelium, while in the case of cartilage it forms the main bulk of the tissue, and the cells only appear as imbedded in, not as cemented by, the intercellular substance.

This intercellular substance may be either homogeneous or fibrillated.

In many cases (*e.g.* the cornea) it can be shown to contain a number of irregular branched cavities, which communicate with each other, and in which the branched cells lie: through these branching spaces nutritive fluids can find their way into the very remotest parts of a non-vascular tissue.

As a special variety of intercellular substance must be mentioned the basement membrane (*membrana propria*) which is found at the base of the epithelial cells in most mucous membranes, and especially as an investing tunic of gland follicles which determines their shape, and which may persist as a hyaline saccule after the gland-cells have all been discharged.

(2) By anastomosis of their processes.

This is the usual way in which stellate cells, *e.g.* of the cornea, are united: the individuality of each cell is thus to a great extent lost by its connection with its neighbours to form a reticulum: as an example of a network so produced, we may cite the stroma of lymphatic glands.

Sometimes the branched processes breaking up into a maze of minute fibrils, adjoining cells are connected by an intermediate reticulum: this is the case in the nerve-cells of the spinal cord.

Besides the Cell, which may be termed the primary tissue-element, there are materials which may be termed secondary or derived tissue-elements. Such are Intercellular substance, Fibres and Tubules.

Intercellular substance is probably in all cases directly derived from the cells themselves. In some cases (*e.g.* cartilage), by the use of re-agents the cementing intercellular substance is, as it were, analysed into various masses, each arranged in concentric ayers around a cell or group of cells, from which it was probably derived (fig. 6).

Fibres.—In the case of the crystalline lens, and of muscle both striated and non-striated, each fibre is simply a metamorphosed cell: in the case of striped fibre the elongation being accompanied by a multiplication of the nuclei.

The various fibres and fibrillæ of connective tissue result from a gradual transformation of an originally homogeneous intercellular substance. Fibres thus formed may undergo great chemical as well as physical transformation: this is notably the case with yellow elastic tissue, in which the sharply defined elastic fibres, possessing great power of resistance to re-agents, contrast strikingly with the homogeneous matter from which they are derived.

Tubules which were originally supposed to consist of structureless membrane, have now been proved to be composed of flat, thin cells, cohering along their edges. (See Capillaries.)

With these simple materials the various parts of the body are built up; the more elementary tissues being, so to speak, first compounded of them; while these again are variously mixed and interwoven to form more intricate combinations.

Thus are constructed epithelium and its modifications, connective tissue, fat, cartilage, bone, the fibres of muscle and nerve, &c.; and these, again, with the more simple structures before mentioned, are used as materials wherewith to form arteries, veins, and lymphatics, secreting and vascular glands, lungs, heart, liver, and other parts of the body.

CHAPTER III.

STRUCTURE OF THE ELEMENTARY TISSUES.

In this chapter the leading characters and chief modifications of two great groups of tissues—the Epithelial and Connective—will be briefly described; while the Nervous and Muscular, together with several other more highly specialized tissues, will be appropriately considered in the chapters treating of their physiology.

Epithelium.

Epithelium is composed of cells of various shapes held together by a small quantity of cementing intercellular substance.

Epithelium clothes the whole exterior surface of the body, forming the *epidermis* with its appendages—nails and hairs; becoming continuous at the chief orifices of the body—nose, mouth, anus, and urethra—with the epithelium which lines the whole length of the alimentary and genito-urinary tracts, together with the ducts of their various glands. Epithelium also lines the cavities of the brain, and the central canal of the spinal cord, the serous and synovial membranes, and the interior of all blood-vessels and lymphatics.

The cells composing it may be arranged in either one or more layers, and thus it may be sub-divided into (*a*) *Simple* and (*b*) *Stratified or laminated Epithelium.* A simple epithelium, for example, lines the whole intestinal mucous membrane from the stomach to the anus: the epidermis on the other hand is laminated throughout its entire extent.

Epithelial cells possess an intracellular and an intranuclear network (p. 11). They are held together by a clear, albuminous, cement substance. The viscid semi-fluid consistency both of cells and intercellular substance permits such changes of shape and arrangement in the individual cells as are necessary if the epithelium is to maintain its integrity in organs the area of whose free surface is so constantly changing, as the stomach, lungs, &c. Thus, if there be but a single layer of cells, as in the epithelium lining the air vesicles of the lungs, the stretching of this membrane causes such a thinning out of the cells that they change their shape from spheroidal or short columnar, to squamous, and *vice versâ,* when the membrane shrinks.

Classification of Epithelial Cells.

Epithelial cells may be conveniently classified as:

1. *Squamous, scaly, pavement, or tesselated.*
2. *Spheroidal, glandular, or polyhedral.*
3. *Columnar, cylindrical, conical, or goblet-shaped.*
4. *Ciliated.*
5. *Transitional.*

Although, for convenience, epithelial cells are thus classified, yet the first three forms of cells are sometimes met with at different depths in the same membrane. As an example of such a laminated epithelium showing these different cell-forms at various depths, we may select the anterior epithelium of the cornea (fig. 11).

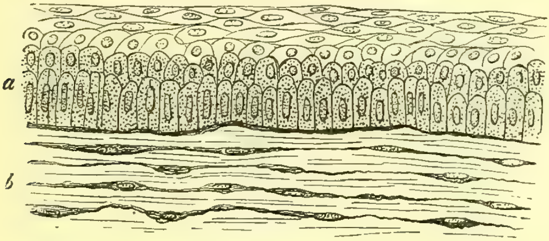


Fig. 11.—*Vertical section of Rabbit's cornea.* *a.* Anterior epithelium, showing the different shapes of the cells at various depths from the free surface. *b.* Portion of the substance of cornea. (Klein.)

1. *Squamous Epithelium* (fig. 12).—Arranged (A) in several superposed layers (*stratified or laminated*), this form of epithelium covers (*a*) the skin, where it is called the Epidermis, and lines (*b*) the mouth, pharynx, and œsophagus, (*c*) the conjunctiva, (*d*) the vagina, and entrance of the urethra in both sexes; while, as (B) a single layer, the same kind of epithelium forms (*a*) the pigmentary layer of the retina, and lines (*b*) the interior of the serous and synovial sacs, and (*c*) of the heart, blood- and lymph-vessels (Endothelium). It consists of cells, which are flattened and scaly, with an irregular outline: and, when laminated, may form a dense horny investment, as on parts of the palms of the hands and soles of the feet. The nucleus is often not apparent. The really cellular nature of even the dry and shrivelled scales cast off from the surface of the epidermis, can be proved by the application of caustic potash, which causes them rapidly to swell and assume their original form.

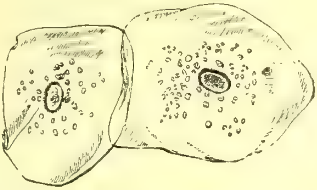


Fig. 12.—*Squamous epithelium scales* from the inside of the mouth. × 260. (Henle.)

Squamous cells are generally united by an intercellular substance; but in many of the deeper layers of epithelium in the mouth and skin, the outline of the cells is very irregular.

Such cells (fig. 13) are termed "ridge and furrow," "cogged" or "prickle" cells. These "prickles" are prolongations of the intracellular network which run across from cell to cell, thus joining them together, the interstices being filled by the transparent intercellular cement substance. When this increases in quantity in inflammation, the cells are pushed further apart and the connecting fibrils or "prickles" elongated, and therefore more clearly visible.

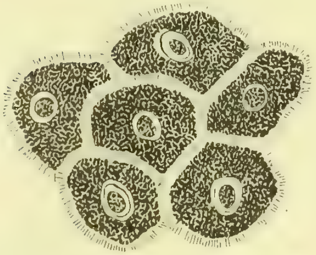


Fig. 13.—*Jagged cells of the middle layers of pavement epithelium,* from a vertical section of the gum of a newborn infant. (Klein.)

Squamous epithelium, *e.g.* the pigment cells of the retina, may have a deposit of pigment in the cell-substance. This pigment consists of minute molecules of *melanin*, imbedded in the cell-substance and almost concealing the nucleus, which is itself transparent (fig. 14).

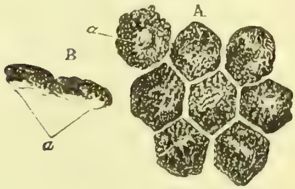


Fig. 14.—*Pigment cells from the retina.* A, cells still cohering, seen on their surface; *a*, nucleus indistinctly seen. In the other cells the nucleus is concealed by the pigment granules. B, two cells seen in profile; *a*, the outer or posterior part containing scarcely any pigment. × 370. (Henle.)

In white rabbits and other albino animals, in which the pigment of the eye is absent, this layer is found to consist of colourless pavement epithelial cells.

Endothelium.—The squamous epithelium lining the serous membranes, and the interior of blood-vessels, presents so many special features as to demand a special description; it is called by a distinct name—Endothelium.

The main points of distinction above alluded to are, 1. the very flattened form of these cells; 2. their constant occurrence in only a single layer; 3. the fact that they are developed from the "mesoblast," while all other epithelial cells are derived from the "epiblast," or "hypoblast;" 4. they line closed cavities not communicating with the exterior of the body. Endothelial cells form an important and well-defined sub-division of squamous epithelial cells, which has been especially studied during the last few years. Their examination has been much facilitated by the adoption of the method of staining serous membranes with silver nitrate.

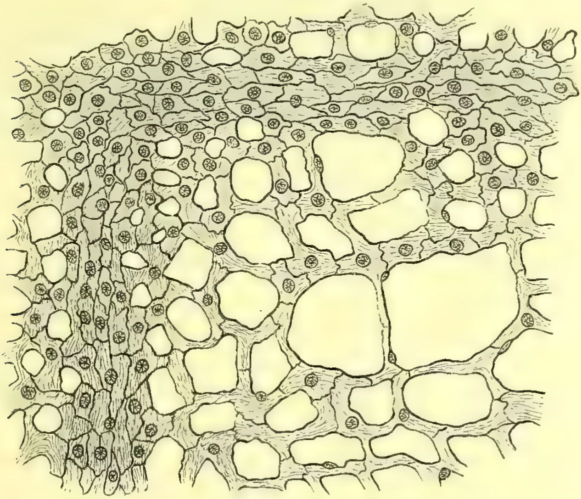


Fig. 15.—*Part of the omentum of a cat*, stained in silver nitrate, × 100. The tissue forms a "*fenestrated membrane*," that is to say, one which is studded with holes or windows. In the figure these are of various shapes and sizes, leaving trabeculæ, the basis of which is fibrous tissue. The trabeculæ are of various sizes, and are covered with endothelial cells, the nuclei of which have been made evident by staining with hæmatoxylin after the silver nitrate has outlined the cells by staining the intercellular substance. (V. D. Harris.)

When a small portion of a perfectly fresh serous membrane, as the mesentery or omentum (fig. 15), is immersed for a few minutes in a quarter per cent. solution of this re-agent, washed with water and exposed to the action of light, the silver oxide is precipitated along the boundaries of the cells, and the whole surface is found to be marked out with exquisite delicacy, by fine dark lines, into a number of polygonal spaces (endothelial cells) (figs. 15 and 16).

Endothelium lines, as before mentioned, all the serous cavities of the body, including the anterior chamber of the eye, also the synovial membranes of joints, and the interior of the heart and of all blood-vessels and lymphatics. It forms also a delicate investing sheath for nerve-fibres and peripheral ganglion-cells. The cells are scaly in form, and irregular in outline ; those lining the interior of blood-vessels and lymphatics having a spindle-shape with a very wavy outline. They enclose a clear, oval nucleus, which, when the cell is viewed in profile, is seen to project from its surface.

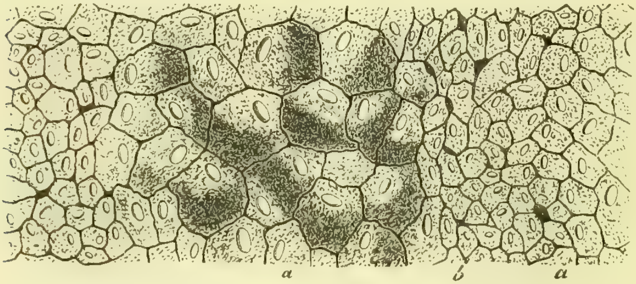


Fig 16.—*Abdominal surface of centrum tendineum of diaphragm of rabbit,* showing the general polygonal shape of the endothelial cells: each is nucleated. (Klein.) × 300.

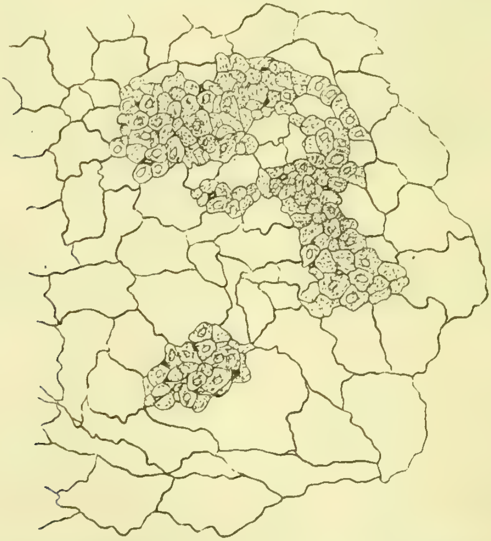


Fig. 17.—*Silver-stained preparation of great omentum of dog,* which shows, amongst the flat endothelium of the surface, small and large groups of germinating endothelium, between which numbers of stomata are to be seen. (Klein.) × 300.

Endothelial cells may be ciliated, *e.g.*, those in the mesentery of frogs, especially about the breeding season.

Besides the ordinary endothelial cells above described, there are found on the omentum and parts of the pleura of many animals, little bud-like processes or nodules, consisting of small polyhedral granular cells, rounded on their free surface, which multiply very rapidly by division (fig. 17). These constitute what is known as "germinating endothelium." The process of germination doubtless goes on in health, and the small cells which are thrown off in succession are carried into the lymphatics, and contribute to the number of the lymph corpuscles. The buds may be enormously increased both in number and size in certain diseased conditions.

On those portions of the peritoneum and other serous membranes where lymphatics abound, there are numerous small orifices—*stomata*—(fig. 18) between the endothelial cells: these are really the open mouths of lymphatic vessels, and through them lymph-corpuscles, and the serous fluid from the serous cavity, pass into the lymphatic system.

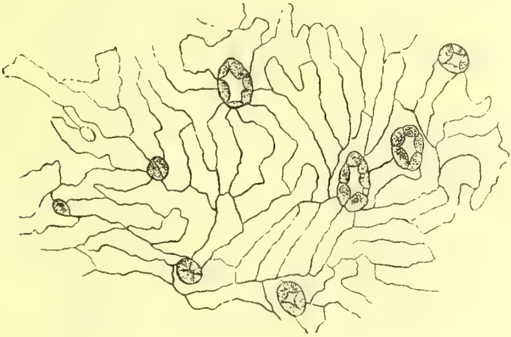


Fig. 18.—*Peritoneal surface of septum cisternæ lymphaticæ magnæ of frog.* The stomata, some of which are open, some collapsed, are surrounded by germinating endothelium. (Klein.) × 160.

2. *Spheroidal* epithelial cells are the active secreting agents in most secreting glands, and hence are often termed glandular; they are generally more or less rounded in outline: often polygonal from mutual pressure.

Excellent examples are to be found in the liver, the secreting tubes of the kidney, and in the salivary and peptic glands (fig. 19).

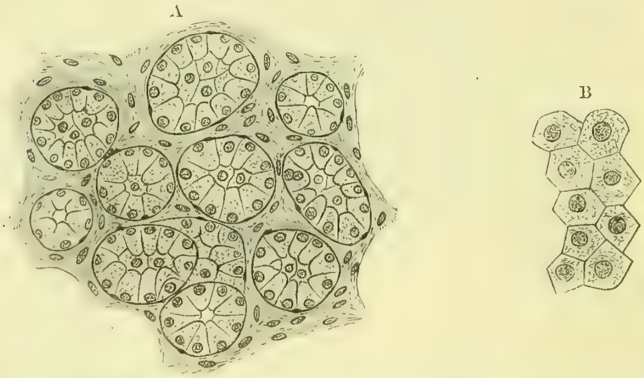


Fig. 19.—*Glandular epithelium.* A, small lobule of a mucous gland of the tongue, showing nucleated glandular spheroidal cells. B. Liver cells. × 200. (V. D. Harris.)

3. *Columnar* epithelium (fig. 20, A and B) lines (a.) the mucous membrane of the stomach and intestines, from the cardiac orifice of the stomach to the anus, and (b.) wholly or in part the ducts of the glands opening on its free surface; also (c.) many gland-ducts in other regions of the body, *e.g.*, mammary, salivary, &c.; (d.) the

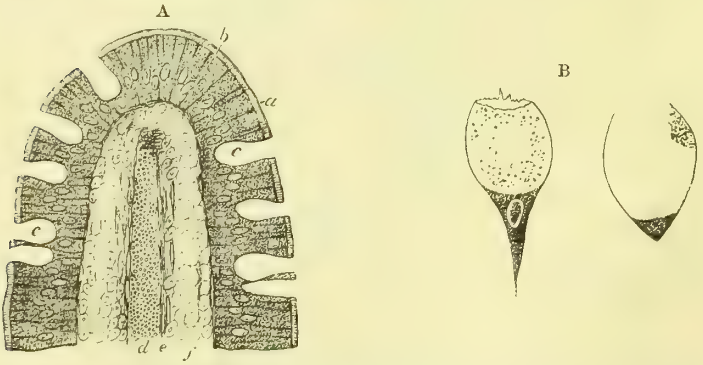


Fig. 20.—A. *Vertical section of a villus* of the small intestine of a cat. *a.* Striated basilar border of the epithelium. *b.* Columnar epithelium. *c.* Goblet cells. *d.* Central lymph-vessel. *e.* Smooth muscular fibres. *f.* Adenoid stroma of the villus in which lymph corpuscles lie. B. *Goblet-cells.* (Klein.)

cells which form the deeper layers of the epithelial lining of the trachea are approximately columnar.

It consists of cells which are cylindrical or prismatic in form, and contain a large oval nucleus. When evenly packed side by side as a single layer, the cells are uniformly columnar; but when occurring in several layers as in the deeper strata of the epithelial lining of the trachea, their shape is very variable, and often departs very widely from the typical columnar form.

Goblet-cells.—Many cylindrical epithelial cells undergo a curious transformation, and from the alteration in their shape are termed goblet-cells (fig. 20, A, *c*, and B).

These are never seen in a perfectly fresh specimen: but if such a specimen be watched for some time, little knobs are seen gradually appearing on the free surface of the epithelium, and are finally detached; these consist of the cell-contents which are discharged by the open mouth of the goblet, leaving the nucleus surrounded by the remains of the protoplasm in its narrow stem.

Some regard this transformation as a normal process which is continually going on during life, the discharged cell-contents contributing to form *mucus*, the cells being supposed in many cases to recover their original shape.

The columnar epithelial cells of the alimentary canal possess a structureless layer on their free surface: such a layer, appearing striated when viewed in section, is termed the "striated basilar border" (fig. 20, A, *a*).

4. *Ciliated* cells are generally cylindrical (fig. 21, B), but may be spheroidal or even almost squamous in shape (fig. 21, A).

This form of epithelium lines (a.) the whole of the respiratory tract from the larynx to the finest sub-divisions of the bronchi, also the lower parts of the nasal passages, and some portions of the generative apparatus—in the male (b.) lining the "vasa efferentia" of the testicle, and their prolongations as far as the lower end of the epididymis; in the female (c.) commencing about the middle of the neck of the uterus, and extending throughout the uterus and Fallopian tubes to their fimbriated extremities, and even for a short distance on the peritoneal surface of the latter. (d.) The ventricles of the brain and the central canal of the spinal cord are clothed with ciliated epithelium in the child, but in the adult it is limited to the central canal of the cord.

The *Cilia*, or fine hair-like processes which give the name to this variety of epithelium, vary a good deal in size in different classes of animals, being very much smaller in the higher than among the lower orders, in which they sometimes exceed in length the cell itself.

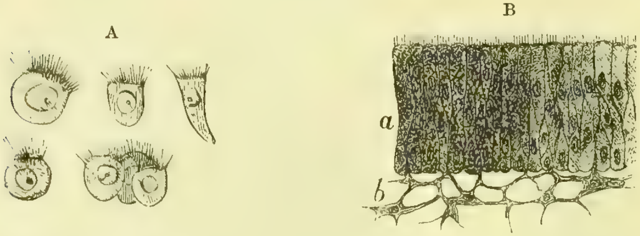


Fig. 21.—A. *Spheroidal ciliated cells* from the mouth of the frog. × 300 diameters. (Sharpey.)
B. *a. Ciliated columnar epithelium* lining a bronchus. *b.* Branched connective-tissue corpuscles. (Klein and Noble Smith.)

The number of cilia on any one cell ranges from ten to thirty, and those attached to the same cell are often of different lengths. When living ciliated epithelium, *e.g.*, the gill of a mussel, is examined under the microscope, the cilia are seen to be in constant rapid motion; each cilium being fixed at one end, and swinging or lashing to and fro. The general impression given to the eye of the observer is very similar to that produced by waves in a field of corn, or swiftly running and rippling water, and the result of their movement is to produce a continuous current in a definite direction, and this direction is invariably the same on the same surface, being always, in the case of a cavity, towards its external orifice.

5. *Transitional Epithelium.*—This term has been applied to cells which are neither arranged in a single layer, as is the case with simple epithelium, nor yet in many superimposed strata as in laminated; in other words, the term is employed when epithelial cells are found in two, three, or four superimposed layers. The upper layer may be either columnar, ciliated, or squamous. When the upper layer is columnar or ciliated, the second layer consists of smaller cells fitted into the inequalities of the cells above them, as in the trachea (fig. 21, B). The epithelium which is met with lining the urinary bladder and ureters is, however, the transitional *par*

excellence. In this variety there are two or three layers of cells, the upper being more or less flattened according to the full or collapsed condition of the organ, their under surface being marked with one or more depressions, into which the heads of the next layer of club-shaped cells fit. Between the lower and narrower parts of the second row of cells, are fixed the irregular cells which constitute the third row, and in like manner sometimes a fourth row (fig. 22). It can be easily understood, therefore, that if a scraping of the mucous membrane of the bladder be teazed, and examined under the microscope, cells of a great variety of forms may be made out (fig. 23). Each cell contains a large nucleus, and the larger and superficial cells often possess two.

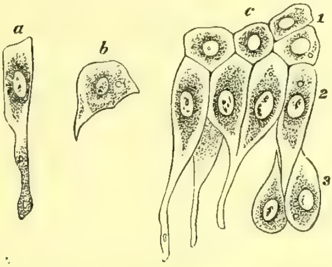


Fig. 22.—*Epithelium of the bladder*; *a*, one of the cells of the first row; *b*, a cell of the second row; *c*, cells *in situ*, of first, second, and deepest layers. (Obersteiner.)

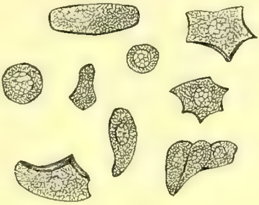


Fig. 23.—*Transitional epithelial cells* from a scraping of the mucous membrane of the bladder of the rabbit. (V. D. Harris.)

Special Epithelium in Organs of Special Sense.—In addition to the above kinds of epithelium, certain highly specialized forms of epithelial cells are found in the organs of smell, sight, and hearing, viz., olfactory cells, retinal rods and cones, auditory cells; they will be described in the chapters which deal with their functions.

Functions of Epithelium.—According to function, epithelial cells may be classified as :—

(1.) *Protective, e.g.*, in the skin, mouth, blood-vessels, &c.

(2.) *Protective and moving*—ciliated epithelium.

(3.) *Secreting*—glandular epithelium ; or, *Secreting formed elements*—epithelium of testicle secreting spermatozoa.

(4.) *Protective and secreting, e.g.*, epithelium of intestine.

(5.) *Sensorial, e.g.*, olfactory cells, rods and cones of retina, organ of Corti.

Epithelium forms a continuous smooth investment over the whole body, being thickened into a hard, horny tissue at the points most exposed to pressure, and developing various appendages, such as hairs and nails, whose structure and functions will be considered in a future chapter. Epithelium lines also the sensorial surfaces of the eye, ear, nose, and mouth, and thus serves as the medium through which all impressions from the external world—touch, smell, taste, sight, hearing—reach the delicate nerve-endings, whence they are conveyed to the brain.

The ciliated epithelium which lines the air-passages serves not only as a protective investment, but also by the movements of its cilia is enabled to propel fluids and minute particles of solid matter so as to aid their expulsion from the body. In the case of the Fallopian tube, this agency assists the progress of the ovum towards the cavity of the uterus. Of the purposes served by cilia in the ventricles of the brain, nothing is known. (For an account of the nature and conditions of ciliary motion, see chapter on Motion.)

The epithelium of the various glands, and of the whole intestinal tract, has the power of *secretion, i.e.*, of chemically transforming certain materials of the blood ; in the case of mucus and saliva this has been proved to involve the transformation of the epithelial cells themselves ; the cell-substance of the epithelial cells of the intestine being discharged by the rupture of their envelopes, as mucus.

Epithelium is likewise concerned in the processes of transudation, diffusion, and absorption.

It is constantly being shed at the free surface, and reproduced in the deeper layers. The various stages of its growth and development can be well seen in a section of any laminated epithelium, such as the epidermis.

The Connective Tissues.

This group of tissues forms the Skeleton with its various connections—bones, cartilages, and ligaments—and also affords a supporting framework and investment to various organs composed of nervous, muscular, and glandular tissue. Its chief function is the mechanical one of support, and for this purpose it is so intimately interwoven with nearly all the textures of the body, that if all other tissues could be removed, and the connective tissues left, we should have a wonderfully exact model of almost every organ and tissue in the body, correct even to the smallest minutiæ of structure.

Classification of Connective Tissues.—The chief varieties of connective tissues may be thus classified :—

I. The Fibrous Connective Tissues.

A.—*Chief Forms.*

a. Areolar.
b. White fibrous.
c. Elastic.

B.—*Special Varieties.*

a. Gelatinous.
b. Adenoid or Retiform.
c. Neuroglia.
d. Adipose.

II. Cartilage.

III. Bone.

All of the varieties of connective tissue are made up of two parts, namely, *cells* and *intercellular substance.*

Cells.—The cells are of two kinds.

(*a.*) *Fixed.*—These are cells of a flattened shape, with branched processes, which are often united together to form a network:

they can be most readily observed in the cornea in which they are arranged, layer above layer, parallel to the free surface. They lie in spaces, in the intercellular or ground substance, which are of the same shape as the cells they contain but rather larger, and which form by anastomosis a system of branching canals freely communicating (fig. 24).

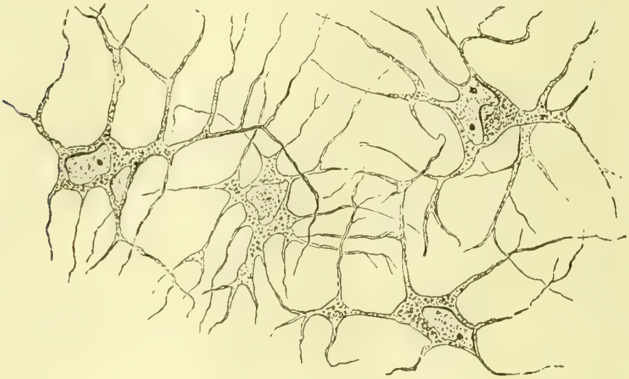


Fig. 24.—*Horizontal preparation of cornea* of frog, stained in gold chloride; showing the network of branched cornea corpuscles. The ground-substance is completely colourless. × 400. (Klein.)

To this class of cells belong the flattened tendon corpuscles which are arranged in long lines or rows parallel to the fibres (fig. 29).

These branched cells, in certain situations, contain a number of pigment-granules, giving them a dark appearance : they form one variety of pigment-cells. Branched pigment-cells of this kind are found in the outer layers of the choroid (fig. 25). In many lower animals, such as the frog, they are found widely distributed, not only in the skin, but also in many internal parts, *e.g.*, the mesentery and sheaths of blood-vessels. In the web of the frog's foot such pigment-cells may be seen, with pigment evenly distributed through the body of the cell and its processes ; but under the action of light, electricity, and other stimuli, the pigment-granules become massed in the body of the cell, leaving the processes quite hyaline ; if the stimulus be removed, they will gradually be distributed again all over the processes. Thus the skin in the frog is sometimes uniformly dusky, and sometimes quite light-coloured, with isolated dark spots. In the choroid and retina the pigment-cells absorb light.

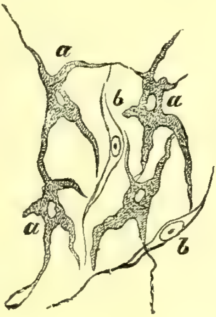


Fig. 25. — *Ramified pigment-cells*, from the tissue of the choroid coat of the eye. × 350. *a*, cell with pigment; *b*, colourless fusiform cells. (Kölliker.)

(*b*.) *Amœboid cells*, of an approximately spherical shape: they have a great general resemblance to colourless blood corpuscles (fig. 2), with which some of them are probably identical. They consist of finely granular nucleated protoplasm, and have the property, not only of changing their form, but also of moving about, whence they are termed migratory. They are readily distinguished from the branched connective-tissue corpuscles by their free condition, and the absence of processes. Some are much larger than others, and are found especially in the sublingual gland of the dog and guinea pig and in the mucous membrane of the intestine. A second variety of these cells called *plasma cells* (Waldeyer) are larger than the amœboid cells, apparently granular, less active in their movements. They are chiefly to be found in the intermuscular septa, in the mucous and submucous coats of the intestine, in lymphatic glands, and in the omentum.

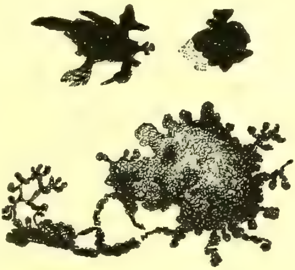


Fig. 26. — *Flat, pigmented, branched, connective-tissue cells* from the sheath of a large blood-vessel of frog's mesentery: the pigment is not distributed uniformly through the substance of the larger cell, consequently some parts of the cell look blacker than others (uncontracted state). In the two smaller cells most of the pigment is withdrawn into the cell-body, so that they appear smaller, blacker, and less branched. × 350. (Klein and Noble Smith.)

Intercellular Substance.—This may be *fibrillar*, as in the fibrous tissues and certain varieties of cartilage; or *homogeneous*, as in hyaline cartilage.

The fibres composing the former are of two kinds—(*a.*) White fibres. (*b.*) Yellow elastic fibres.

(*a.*) *White Fibres.*—These are arranged parallel to each other in wavy bundles of various sizes: such bundles may either have a parallel arrangement (fig. 27), or may produce quite a felted texture by their interlacement. The individual fibres composing these fasciculi are homogeneous, unbranched, and of the same diameter throughout. They can readily be isolated by macerating a portion of white fibrous tissue (*e.g.*, a small piece of tendon) for a short time in lime, or baryta-water, or in a solution of common salt, or potassium permanganate: these reagents possessing the power of dissolving the cementing interfibrillar substance (which is nearly allied to syntonin), and thus separating the fibres from each other.

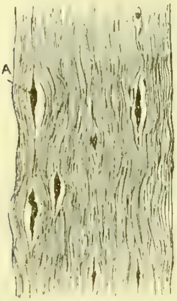


Fig. 27.—*Fibrous tissue of cornea*, showing bundles of fibres with a few scattered fusiform cells lying in the inter-fascicular spaces. × 400. (Klein and Noble Smith.)

(*b.*) *Yellow Elastic Fibres* (fig. 28) are of all sizes, from excessively fine fibrils up to fibres of considerable thickness: they are distinguished from white fibres by the following characters:—(1.) Their great power of resistance even to the prolonged action of chemical reagents, *e.g.*, Caustic Soda, Acetic Acid, &c. (2.) Their well-defined outlines. (3.) Their great tendency to branch and form networks by anastomosis. (4.) They very often have a twisted corkscrew-like appearance, and their free ends usually curl up. (5.) They are of a yellowish tint and very elastic.

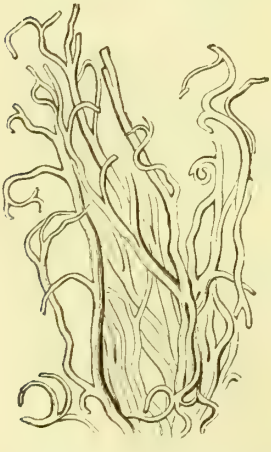


Fig. 28.—*Elastic fibres* from the ligamenta subflava. × 200. (Sharpey.)

Varieties of Connective Tissue.

I. Fibrous Connective Tissues.

A.—*Chief Forms.*—(*a.*) *Areolar Tissue.*

Distribution.—This variety has a very wide distribution, and constitutes the subcutaneous, subserous and submucous tissue. It is found in the mucous membranes, in the true skin, in the outer sheaths of the blood-vessels. It forms sheaths for muscles, nerves, glands, and the internal organs, and, penetrating into their interior, supports and connects the finest parts.

Structure.—To the naked eye it appears, when stretched out, as a fleecy, white, and soft meshwork of fine fibrils, with here and there wider films joining in it, the whole tissue being evidently elastic. The openness of the meshwork varies with the locality from which the specimen is taken. On the addition of acetic acid the tissue swells up, and becomes gelatinous in appearance. Under the microscope it is found to be made up of fine white fibres, which interlace in a most irregular manner, together with a variable number of elastic fibres. These latter resist the action of acetic acid as above mentioned, so that when this reagent is added to a specimen of areolar tissue, although the white fibres swell up and become homogeneous, certain elastic fibres may still be seen arranged in various directions, sometimes even appearing to pass in a more or less circular or in a spiral manner round a small mass of the gelatinous mass of changed white fibres. The cells of the tissue are arranged in no very regular manner, being contained in the spaces (areolæ) between the fibres. They communicate, however, with one another by their branched processes, and also apparently with the cells forming the walls of the capillary blood-vessels in their neighbourhood, connecting together the fibrils in a certain amount of albuminous *cement* substance.

(*b.*) *White Fibrous Tissue.*

Distribution.—Typically in tendon; in ligaments, in the periosteum and perichondrium, the dura mater, the pericardium, the sclerotic coat of the eye, the fibrous sheath of the testicle ; in the fasciæ and aponeurosis of muscles, and in the sheaths of lymphatic glands.

Structure.—To the naked eye, tendons and many of the fibrous membranes, when in a fresh state, present an appearance as of watered silk. This is due to the arrangement of the fibres in wavy parallel bundles. Under the microscope, the tissue appears to consist of long, often parallel, wavy bundles of fibres of different sizes. Sometimes the fibres intersect each other. The cells in tendons are arranged in long chains in the ground substance separating the bundles of fibres, and are more or less regularly quadrilateral with large round nuclei containing nucleoli, which are generally placed so as to be contiguous in two cells. The cells consist of a body, which is thick, from which processes pass in various directions into, and partially filling up the spaces between the bundles of fibres. The rows of cells are separated from one another by lines of cement substance. The cell spaces can be brought into view by silver nitrate. The cells are generally marked by one or more lines or stripes when viewed longitudinally. This appearance is really produced by the laminar extension either projecting upwards or downwards.

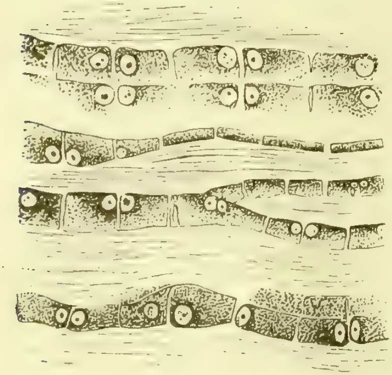


Fig. 29.—*Caudal tendon of young rat*, showing the arrangement, form, and structure of the tendon cells. × 300. (Klein.)

(c.) Yellow Elastic Tissue.

Distribution.—In the ligamentum nuchæ of the ox, horse, and many other animals ; in the ligamenta subflava of man ; in the arteries, constituting the fenestrated coat of Henle ; in veins ; in the lungs and trachea ; in the stylo-hyoid, thyro-hyoid, and crico-thyroid ligaments ; in the true vocal cords.

Structure.—Elastic tissue occurs in various forms, from a structureless, elastic membrane to a tissue whose chief constituents are bundles of elastic fibres crossing each other at different angles: these varieties may be classified as follows:—

(*a.*) Fine elastic fibrils, which branch and anastomose to form a network: this variety of elastic tissue occurs chiefly in the skin and mucous membranes, in subcutaneous and submucous tissue, in the lungs and true vocal cords.

(*b.*) Thick fibres, sometimes cylindrical, sometimes flattened like tape, which branch and form a network: these are seen most typically in the ligamenta subflava and also in the ligamentum nuchæ of such animals as the ox and horse, in which it is largely developed.

(*c.*) Elastic membranes with perforations, *e.g.*, Henle's fenestrated membrane: this variety is found chiefly in the arteries and veins.

(*d.*) Continuous, homogeneous elastic membranes, *e.g.*, Bowman's anterior elastic lamina, and Descemet's posterior elastic lamina, both in the cornea.

A certain number of flat connective tissue cells are found in the ground substance between the elastic fibres constituting this variety of connective tissue.

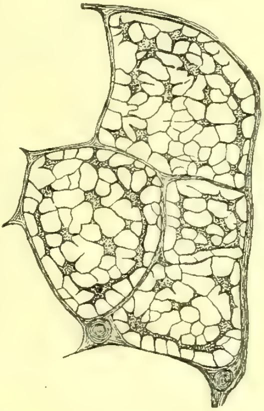


Fig. 30.—*Transverse section of tendon* from a cross section of the tail of a rabbit, showing sheath, fibrous septa, and branched connective-tissue corpuscles. The spaces left white in the drawing represent the tendinous fibres in transverse section. × 250. (Klein.)

B.—*Special Forms.*—(*a.*) *Gelatinous Tissue.*

Distribution.—Gelatinous connective tissue forms the chief part of the bodies of jelly fish; it is found in many parts of the human embryo, but remains in the adult only in the vitreous humour of the eye. It may be best seen in the last-named situation, in the "Whartonian jelly" of the umbilical cord, and in the enamel organ of developing teeth.

Structure.—It consists of cells, which in the vitreous humour are rounded, and in the jelly of the enamel organ are stellate, imbedded in a soft jelly-like inter-cellular substance which forms the bulk of the tissue, and which contains a considerable quantity of mucin. In the umbilical cord, that part of the jelly immediately surrounding the stellate cells shows marks of obscure fibrillation.

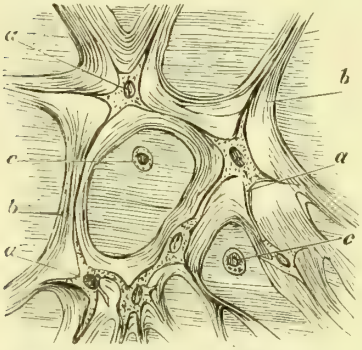


Fig. 31.—*Tissue of the jelly of Wharton* from umbilical cord. *a*, connective-tissue corpuscles; *b*, fasciculi of connective tissue; *c*, spherical formative cells. (Frey.)

(*b.*) *Adenoid or Retiform.*

Distribution.—It composes the stroma of the spleen and lymphatic glands, and is found also in the thymus, in the tonsils, in the follicular glands of the tongue, in Peyer's patches and in the solitary glands of the intestines, and in the mucous membranes generally.

Structure. — Adenoid or retiform tissue consists of a very delicate network of minute fibrils, formed originally by the union of processes of branched connective-tissue corpuscles the nuclei of which, however, are visible only during the early periods of development of the tissue (fig. 32).

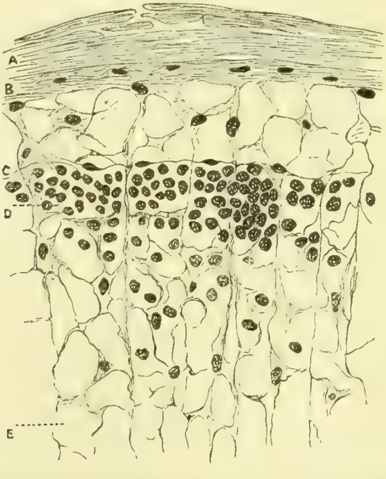


Fig. 32.—*Part of a section of a lymphatic gland*, from which the corpuscles have been for the most part removed, showing the adenoid reticulum. (Klein and Noble Smith.)

The nuclei found on the fibrillar meshwork do not form an essential part of it. The fibrils are neither white fibrous nor elastic tissue, as they are insoluble in boiling water, although readily soluble in hot alkaline solutions.

(*c.*) *Neuroglia.*—This tissue forms the support of the Nervous elements in the Brain and Spinal cord. It consists of a very fine meshwork of fibrils, said to be elastic, and with nucleated plates which constitute the connective-tissue corpuscles imbedded in it.

Development of Fibrous Tissues.—In the embryo the place of the fibrous tissues is at first occupied by a mass of roundish cells, derived from the "mesoblast."

These develop either into a network of branched cells, or into groups of fusiform cells (fig. 33).

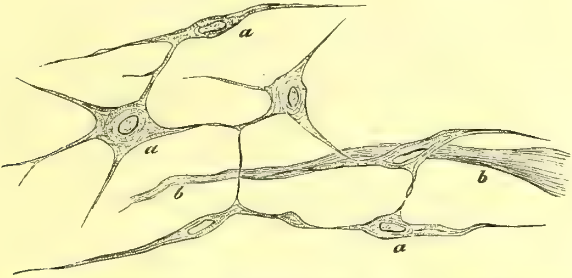


Fig. 33.—*Portion of submucous tissue of gravid uterus of sow.* *a*, branched cells, more or less spindle-shaped; *b*, bundles of connective tissue. (Klein.)

The cells are imbedded in a semi-fluid albuminous substance derived either from the cells themselves or from the neighbouring blood-vessels; this afterwards forms the cement substance. In it fibres are developed, either by part of the cells becoming fibrils, the others remaining as connective-tissue corpuscles, or by the fibrils being developed from the outside layers of the protoplasm of the cells, which grow up again to their original size and remain imbedded among the fibres. This process gives rise to fibres arranged in the one case in interlacing networks (areolar tissue), in the other in parallel bundles (white fibrous tissue). In the mature forms of purely fibrous tissue not only the remnants of the cell-substance, but even the nuclei may disappear. The embryonic tissue, from which *elastic* fibres are developed, is composed of fusiform cells, and a structureless intercellular substance by the gradual fibrillation of which elastic fibres are formed. The fusiform cells dwindle in size and eventually disappear so completely that in mature elastic tissue hardly a trace of them is to be found : meanwhile the elastic fibres steadily increase in size.

Another theory of the development of the connective-tissue fibrils supposes that they arise from deposits in the intercellular substance and not from the cells themselves ; these deposits, in the case of elastic fibres, appearing first of all in the form of rows of granules, which, joining together, form long fibrils. It seems probable that even if this view be correct, the cells themselves have a considerable influence in the production of the deposits outside them.

Functions of Areolar and Fibrous Tissue.—The main function of connective tissue is mechanical rather than vital : it fulfils the subsidiary but important use of supporting and connecting the various tissues and organs of the body.

In glands the trabeculæ of connective tissue form an interstitial framework in which the parenchyma or secreting gland-tissue is lodged: in muscles and nerves the septa of connective tissue support the bundles of fibres, which form the essential part of the structure.

Elastic tissue, by virtue of its elasticity, has other important uses : these, again, are mechanical rather than vital. Thus the ligamentum nuchæ of the horse or ox acts very much as an India-rubber band in the same position would. It maintains the head in a proper position without any muscular exertion ; and when the head has been lowered by the action of the flexor muscles of the neck, and the ligamentum nuchæ thus stretched, the head is brought up again to its normal position by the relaxation of the flexor muscles which allows the elasticity of the ligamentum nuchæ to come again into play.

(*d.*) *Adipose Tissue.*

Distribution.—In almost all regions of the human body a larger or smaller quantity of adipose or fatty tissue is present ; the chief exceptions being the subcutaneous tissue of the eyelids, penis, and scrotum, the nymphæ, and the cavity of the cranium. Adipose *tissue* is also absent from the substance of many organs, as the lungs, liver, and others.

Fatty matter, not in the form of a distinct tissue, is also widely present in the body, *e.g.*, in the liver and brain, and in the blood and chyle.

Adipose tissue is almost always found seated in areolar tissue, and forms in its meshes little masses of unequal size and irregular shape, to which the term *lobules* is commonly applied.

Structure.—Under the microscope adipose tissue is found to consist essentially of little vesicles or cells which present dark, sharply-defined edges when viewed with transmitted light: they are about $\frac{1}{400}$ or $\frac{1}{500}$ of an inch in diameter, each composed of a structureless and colourless membrane or bag, filled with fatty matter, which is liquid during life, but in part solidified after death (fig. 34). A nucleus is always present in some part or other of the cell-wall, but in the ordinary condition of the cell it is not easily or always visible.

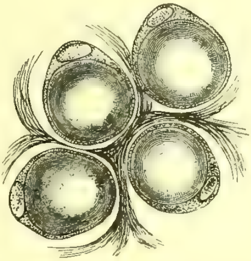


Fig. 34.—*Ordinary fat-cells of a fat tract* in the omentum of a rat. (Klein.)

This membrane and the nucleus can generally be brought into view by staining the tissue: it can be still more satisfactorily demonstrated by extracting the contents of the fat-cells with ether, when the shrunken, shrivelled membranes remain behind. By mutual pressure, fat-cells come to assume a polyhedral figure (fig. 35).

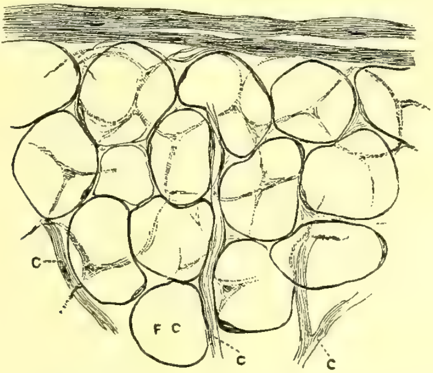


Fig. 35.—*Group of fat-cells* (FC) *with capillary vessels* (C). (Noble Smith.)

The ultimate cells are held together by capillary blood-vessels (fig. 35); while the little clusters thus formed are grouped into small masses, and held so, in most cases, by areolar tissue.

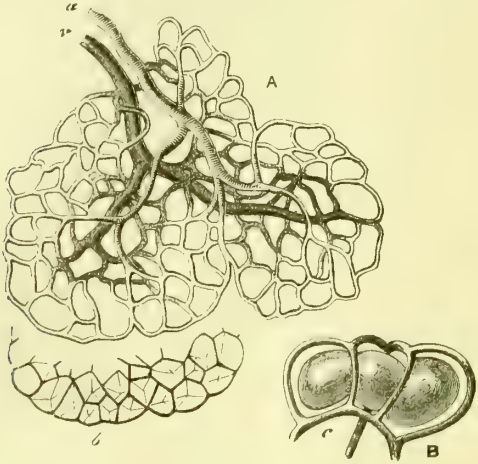


Fig. 36.—*Blood-vessels of adipose tissue.* A. Minute flattened fat-lobule, in which the vessels only are represented. *a*, the terminal artery; *v*, the primitive vein; *b*, the fat-vesicles of one border of the lobule separately represented. × 100. B. Plan of the arrangement of the capillaries (*c*) on the exterior of the vesicles: more highly magnified. (Todd and Bowman.)

The oily matter contained in the cells is composed chiefly of the compounds of fatty acids with glycerin, which are named *olein*, *stearin*, and *palmitin*.

Development of Adipose Tissue.—Fat-cells are developed from connective-tissue corpuscles: in the infra-orbital connective-tissue cells may be found exhibiting every intermediate gradation between an ordinary branched connective-tissue corpuscle and a mature fat-cell. The process of development is as follows: a few small drops of oil make their appearance in the protoplasm: by their confluence a larger drop is produced (fig. 37): this gradually increases in size at the expense of the original protoplasm of the cell, which becomes correspondingly diminished in quantity till in the mature cell it only forms a thin crescentic film, closely pressed against the cell-wall, and with a nucleus imbedded in its substance (figs. 34 and 37).

Under certain circumstances this process may be reversed and fat-cells may be changed back into connective-tissue corpuscles. (Kölliker, Virchow.)

Vessels and Nerves.—A large number of blood-vessels are found in adipose tissue, which subdivide until each lobule of fat contains a fine meshwork of capillaries ensheathing each individual fat-globule. Although nerve fibres pass through the tissue, no nerves have been demonstrated to terminate in it.

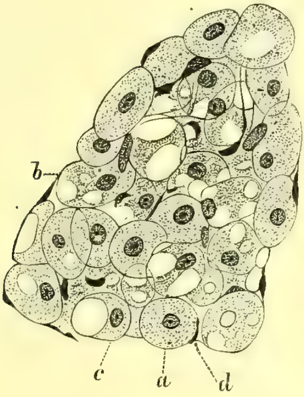


Fig. 37.—*A lobule of developing adipose tissue* from an eight months' fœtus. *a.* Spherical or, from pressure, polyhedral cells with large central nucleus, surrounded by a finely reticulated substance staining uniformly with hæmatoxylin. *b.* Similar cells with spaces from which the fat has been removed by oil of cloves. *c.* Similar cells showing how the nucleus with enclosing protoplasm is being pressed towards periphery. *d.* Nucleus of endothelium of investing capillaries. (McCarthy.) Drawn by Treves.

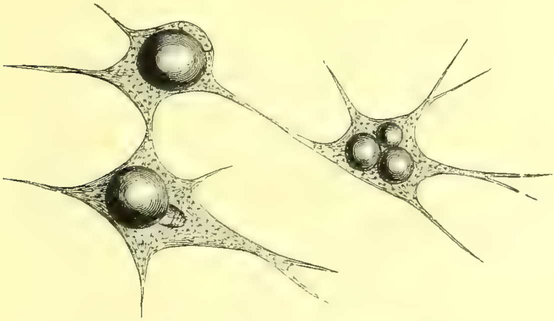


Fig. 38.—*Branched connective-tissue corpuscles, developing into fat-cells.* (Klein.)

The Uses of Adipose Tissue.—Among the uses of adipose tissue, these are the chief:—

a. It serves as a store of combustible matter which may be re-absorbed into the blood when occasion requires, and, being burnt, may help to preserve the heat of the body.

b. That part of the fat which is situate beneath the skin must, by its want of conducting power, assist in preventing undue waste of the heat of the body by escape from the surface.

c. As a packing material, fat serves very admirably to fill up spaces, to form a soft and yielding yet elastic material wherewith to wrap tender and delicate structures, or form a bed with like qualities on which such structures may lie, not endangered by pressure.

As good examples of situations in which fat serves such purposes may be mentioned the palms of the hands and soles of the feet, and the orbits.

d. In the long bones, fatty tissue, in the form known as yellow marrow, fills the medullary canal, and supports the small blood-vessels which are distributed from it to the inner part of the substance of the bone.

II. CARTILAGE.

Cartilage or gristle exists in three different forms in the human body, viz., 1, *Hyaline cartilage*, 2, *Yellow elastic-cartilage*, and 3, *White fibro-cartilage.*

Structure of Cartilage.—All kinds of cartilage are composed of cells imbedded in a substance called the *matrix* : and the apparent differences of structure met with in the various kinds of cartilage are more due to differences in the character of the matrix than of the cells. Among the latter, however, there is also considerable diversity of form and size.

With the exception of the articular variety, cartilage is invested by a thin but tough firm fibrous membrane called the *perichondrium.* On the surface of the articular cartilage of the fœtus, the perichondrium is represented by a film of epithelium ; but this is gradually worn away up to the margin of the articular surfaces, when by use the parts begin to suffer friction.

Nerves are probably not supplied to any variety of cartilage.

1. Hyaline Cartilage.

Distribution.—This variety of cartilage is met with largely in the human body—investing the articular ends of bones, and forming the costal cartilages, the nasal cartilages, and those of the larynx with the exception of the epiglottis and cornicula laryngis. The cartilages of the trachea and bronchi are also hyaline.

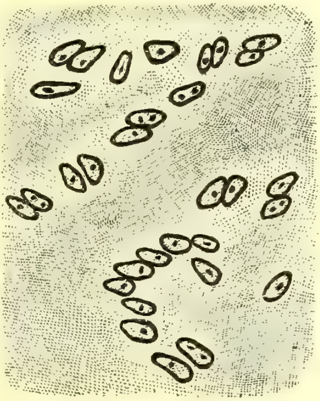


Fig. 39. — *Ordinary hyaline cartilage* from trachea of a child. The cartilage cells are enclosed singly or in pairs in a capsule of hyaline substance. × 150 diams. (Klein and Noble Smith.)

Structure.—Like other cartilages it is composed of cells imbedded in a matrix. The cells, which contain a nucleus with nucleoli, are irregular in shape, and generally grouped together in patches (fig. 39). The patches are of various shapes and sizes, and placed at unequal distances apart. They generally appear flattened near the free surface of the mass of cartilage in which they are placed, and more or less perpendicular to the surface in the more-deeply seated portions.

The matrix of hyaline cartilage has a dimly granular appearance like that of ground glass, and in man and the higher animals has no apparent structure. In some cartilages of the frog, however, even when examined in the fresh state, it is

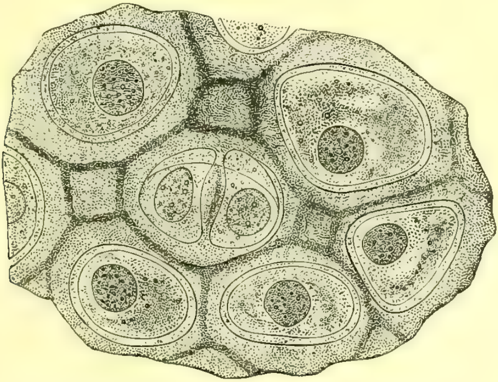


Fig. 40.—*Fresh cartilage from the Triton.* (A. Rollett.)

seen to be mapped out into polygonal blocks or cell-territories, each containing a cell in the centre, and representing what is generally called the capsule of the cartilage cells (fig. 40). Hyaline cartilage in man has really the same structure, which can be demonstrated by the use of certain reagents. If a piece of human hyaline cartilage be macerated for a long time in dilute acid or in hot water 95°—113° F. (35° to 45° C.), the matrix, which previously appeared quite homogeneous, is found to be resolved into a number of concentric lamellæ, like the coats of an onion, arranged round each cell or group of cells. It is thus shown to consist of nothing but a number of large systems of capsules which have become fused with one another.

The cavities in the matrix in which the cells lie are connected together by a series of branching canals, very much resembling those in the cornea : through these canals fluids may make their way into the depths of the tissue.

In the hyaline cartilage of the ribs, the cells are mostly larger than in the articular variety, and there is a tendency to the development of fibres in the matrix. The costal cartilages also frequently become calcified in old age, as also do some of those of the larynx. Fat-globules may also be seen in many cartilages.

In articular cartilage the cells are smaller, and arranged vertically in narrow lines like strings of beads.

Temporary Cartilage.—In the fœtus, cartilage is the material of which the bones are first constructed ; the "model" of each bone being laid down, so to speak, in this substance. In such cases the cartilage is termed *temporary.* It closely resembles the ordinary hyaline kind ; the cells, however, are not grouped together after the fashion just described, but are more uniformly distributed throughout the matrix.

A variety of temporary hyaline cartilage which has scarcely any matrix is found in the human subject only in early fœtal life, when it constitutes the *chorda dorsalis.*

Nutrition of Cartilage. — Hyaline cartilage is reckoned among the so-called *non-vascular* structures, no blood-vessels being supplied directly to its own substance ; it is nourished by those of the bone beneath. When hyaline cartilage is in thicker masses, as in the case of the cartilages of the ribs, a few blood-vessels traverse its substance. The distinction, however, between all so-called *vascular* and *non-vascular* parts, is at the best a very artificial one.

2. Yellow Elastic Cartilage.

Distribution.—In the external ear, in the epiglottis and cornicula laryngis, and in the Eustachian tube.

Structure.—The cells are rounded or oval, with well-marked nuclei and nucleoli (fig. 41). The matrix in which they are seated is composed almost entirely of fine elastic fibres, which form an intricate interlacement about the cells, and in their general characters are allied to the yellow variety of fibrous tissue: a small and variable quantity of hyaline intercellular substance is also usually present.

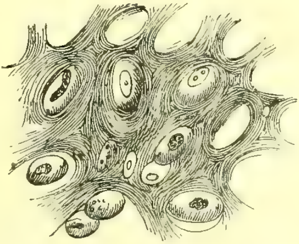


Fig. 41.—*Section of the epiglottis.* (Baly.)

A variety of elastic cartilage, sometimes called *cellular*, may be obtained from the external ear of rats, mice, or other small mammals. It is composed almost entirely of cells (hence the name), which are packed very closely, with little or no matrix. When present the matrix consists of very fine fibres, which twine about the cells in various directions and enclose them in a kind of network.

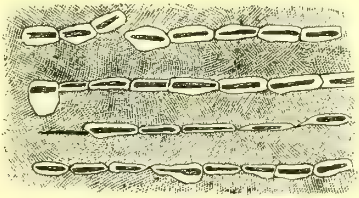


Fig. 42.—*Transverse section through the intervertebral cartilage* of tail of mouse, showing lamellæ of fibrous tissue with cartilage cells arranged in rows between them. The cells are seen in profile, and being flattened, appear staff-shaped. Each cell lies in a capsule. × 350. (Klein and Noble Smith.)

3. White Fibro-Cartilage.

Distribution.—The different situations in which white fibro-cartilage is found have given rise to the following classification:—

1. *Inter-articular* fibro-cartilage, *e.g.*, the semilunar cartilages of the knee-joint.

2. *Circumferential* or marginal, as on the edges of the acetabulum and glenoid cavity.

3. *Connecting, e.g.*, the inter-vertebral fibro-cartilages.

4. In the *sheaths of tendons*, and sometimes in their substance. In the latter situation, the nodule of fibro-cartilage is called a *sesamoid* fibro-cartilage, of which a specimen may be found in the tendon of the tibialis posticus, in the sole of the foot, and usually in the neighbouring tendon of the peroneus longus.

Structure.—White fibro-cartilage (fig. 43), which is much more widely distributed throughout the body than the foregoing kind, is composed, like it, of cells and a matrix; the latter, however, being made up almost entirely of fibres closely resembling those of white fibrous tissue.

In this kind of fibro-cartilage it is not unusual to find a great part of its mass composed almost exclusively of fibres, and deriving the name of cartilage only from the fact that in another portion, continuous with it, cartilage cells may be pretty freely distributed.

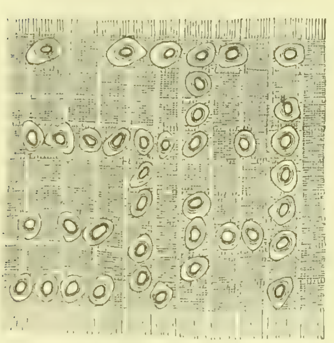


Fig. 43.—*White fibro-cartilage* from an inter-vertebral ligament. (Klein and Noble Smith.)

Functions of Cartilage.—Cartilage not only represents in the fœtus the bones which are to be formed (temporary cartilage), but also offers a firm, but more or less yielding, framework for certain parts in the developed body, possessing at the same time strength and elasticity. It maintains the shape of tubes as in the larynx and trachea. It affords attachment to muscles and ligaments; it binds bones together, yet allows a certain degree of movement, as between the vertebræ; it forms a firm framework and protection, yet without undue stiffness or weight, as in the pinna, larynx, and chest walls; it deepens joint cavities, as in the acetabulum, without unduly restricting the movements of the bones.

Development of Cartilage.—Cartilage is developed out of an embryonal tissue, consisting of cells with a very small quantity of intercellular substance: the cells multiply by fission within the cell-capsules (fig. 6); while the capsule of the parent cell becomes gradually fused with the surrounding intercellular substance. A repetition of this process in the young cells causes a rapid growth of the cartilage by the multiplication of its cellular elements and corresponding increase in its matrix.

III. Bone.

Chemical Composition.—Bone is composed of *earthy* and *animal* matter in the proportion of about 67 per cent. of the former to 33 per cent. of the latter. The earthy matter is composed chiefly of calcium phosphate, but besides there is a small quantity (about 11 of the 67 per cent.) of calcium carbonate and fluoride, and magnesium phosphate.

The animal matter is resolved into *gelatin* by boiling.

The earthy and animal constituents of bone are so intimately blended and incorporated the one with the other, that it is only by chemical action, as, for instance, by heat in one case and by the action of acids in another, that they can be separated. Their close union, too, is further shown by the fact that when by acids the earthy matter is dissolved out, or, on the other hand, when the animal part is burnt out, the shape of the bone is alike preserved.

The proportion between these two constituents of bone varies in different bones in the same individual, and in the same bone at different ages.

Structure.—To the naked eye there appear two kinds of structure in different bones, and in different parts of the same bone, namely, the *dense* or *compact*, and the *spongy or cancellous* tissue.

Thus, in making a longitudinal section of a long bone, as the humerus or femur, the articular extremities are found capped on their surface by a thin shell of compact bone, while their interior is made up of the spongy or cancellous tissue. The *shaft*, on the other hand, is formed almost entirely of a thick layer of the compact bone, and this surrounds a central canal, the *medullary* cavity—so called from its containing the *medulla* or marrow.

In the flat bones, as the parietal bone or the scapula, one layer of the cancellous structure lies between two layers of the compact tissue, and in the short and irregular bones, as those of the *carpus* and *tarsus*, the cancellous tissue alone fills the interior, while a thin shell of compact bone forms the outside.

Marrow.—There are two distinct varieties of marrow—the *red* and *yellow.*

Red marrow is that variety which occupies the spaces in the cancellous tissue; it is highly vascular, and thus maintains the nutrition of the spongy bone, the interstices of which it fills. It contains a few fat-cells and a large number of marrow-cells, many of which are undistinguishable from lymphoid corpuscles, and has for a basis a small amount of fibrous tissue. Among the cells are some nucleated cells of very much the same tint as coloured blood-corpuscles. There are also a few large cells with many nuclei, termed "giant-cells" (myeloplaxes), which are derived from over-growth of the ordinary marrow-cells (fig. 44).

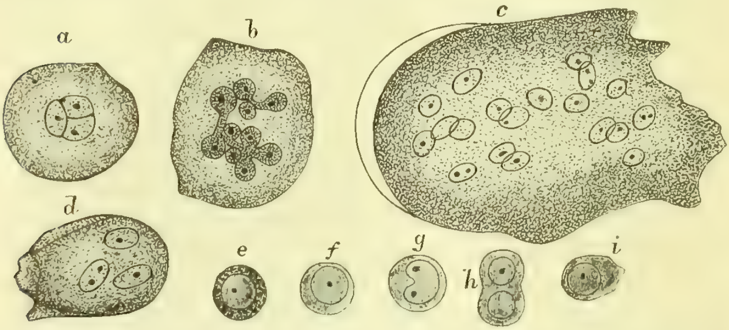


Fig. 44.—*Cells of the red marrow of the guinea pig*, highly magnified. *a*, a large cell, the nucleus of which appears to be partly divided into three by constrictions; *b*, a cell, the nucleus of which shows an appearance of being constricted into a number of smaller nuclei; *c*, a so-called giant cell, or myeloplaxe, with many nuclei; *d*, a smaller myeloplaxe, with three nuclei; *e*—*i*, proper cells of the marrow. (E. A. Schäfer.)

Yellow marrow fills the medullary cavity of long bones, and consists chiefly of fat-cells with numerous blood-vessels; many of its cells also are in every respect similar to lymphoid corpuscles.

From these marrow-cells, especially those of the red marrow, are derived, as we shall presently show, large quantities of red blood-corpuscles.

Periosteum and Nutrient Blood-vessels.—The surfaces of bones, except the part covered with articular cartilage, are clothed by a tough, fibrous membrane, the *periosteum;* and it is from the blood-vessels which are distributed in this membrane, that the bones, especially their more compact tissue, are in great part supplied with nourishment,—minute branches from the periosteal vessels entering the little foramina on the surface of the bone, and finding their way to the Haversian canals, to be immediately described. The long bones are supplied also by a proper nutrient artery which, entering at some part of the shaft so as to reach the medullary canal, breaks up into branches for the supply of the marrow, from which again small vessels are distributed to the interior of the bone. Other small blood-vessels pierce the articular extremities for the supply of the cancellous tissue.

Microscopic Structure of Bone.—Notwithstanding the differences of arrangement just mentioned, the structure of all bone is found under the microscope to be essentially the same.

Examined with a rather high power its substance is found to contain a multitude of little irregular spaces, approximately fusiform in shape, called *lacunæ*, with very minute canals or *canaliculi*, as they are termed, leading from them, and anastomosing with similar little prolongations from other lacunæ (fig. 45).

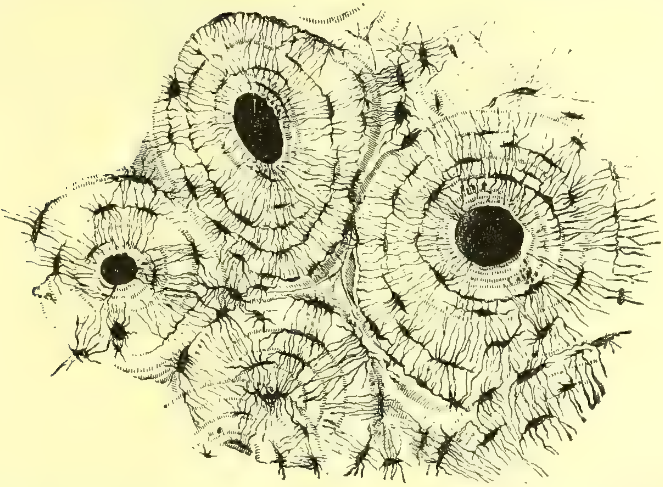


Fig. 45.—*Transverse section of compact bony tissue* (of humerus). Three of the Haversian canals are seen, with their concentric rings; also the corpuscles or lacunæ, with the canaliculi extending from them across the direction of the lamellæ. The Haversian apertures had got filled with debris in grinding down the section, and therefore appear black in the figure, which represents the object as viewed with transmitted light. The Haversian systems are so closely packed in this section, that scarcely any *interstitial* lamellæ are visible. × 150. (Sharpey.)

In very thin layers of bone, no other canals than these may be visible; but on making a transverse section of the compact tissue as of a long bone, *e.g.*, the humerus or ulna, the arrangement shown in fig. 45, can be seen.

The bone seems mapped out into small circular districts, at or about the centre of each of which is a hole, and around this an appearance as of concentric layers—the *lacunæ* and *canaliculi* following the same concentric plan of distribution around the small hole in the centre, with which, indeed, they communicate.

On making a longitudinal section, the central holes are found to be simply the cut extremities of small canals which run lengthwise through the bone, anastomosing with each other by lateral branches (fig. 46), and are called Haversian canals, after the name of the physician, Clopton Havers, who first accurately described them. The Haversian canals, the average diameter of which is $\frac{1}{500}$ of an inch, contain blood-vessels, and by means of them blood is conveyed to all, even the densest parts of the bone; the minute canaliculi and lacunæ absorbing nutrient matter from the Haversian blood-vessels, and conveying it still more intimately to the very substance of the bone which they traverse.

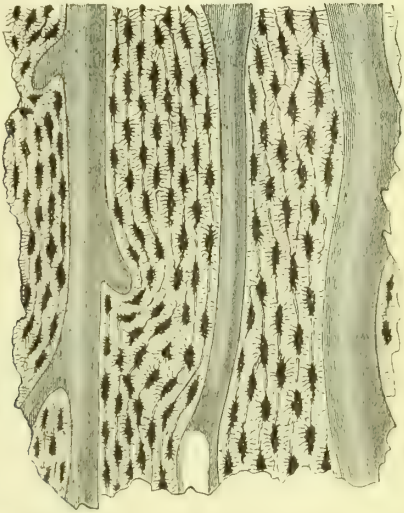


Fig. 46.—*Longitudinal section of human ulna*, showing Haversian canal, lacunæ, and canaliculi. (Rollett.)

The blood-vessels enter the Haversian canals both from without, by traversing the small holes which exist on the surface of all bones beneath the periosteum, and from within by means of small channels which extend from the medullary cavity, or from the cancellous tissue. The arteries and veins usually occupy separate canals, and the veins, which are the larger, often present, at irregular intervals, small pouch-like dilatations.

The *lacunæ* are occupied by branched cells (bone-cells, or bone-corpuscles) (fig. 47), which very closely resemble the ordinary branched connective-tissue corpuscles; each of these little masses of protoplasm ministering to the nutrition of the bone immediately surrounding it, and one lacunar corpuscle communicating with another, and with its surrounding district, and with the blood-vessels of the Haversian canals, by means of the minute streams of fluid nutrient matter which occupy the canaliculi.

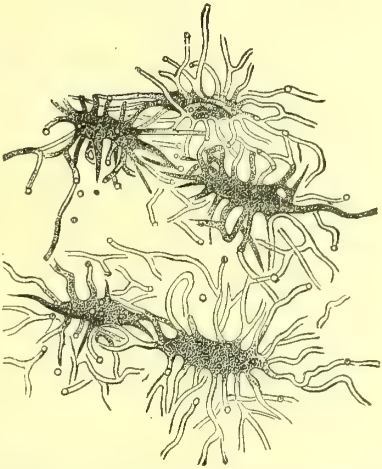


Fig. 47.—*Bone corpuscles* with their processes as seen in a thin section of human bone. (Rollett.)

It will be seen from the above discription that bone is essentially connective-tissue impregnated with lime salts: it bears a very close resemblance to what may be termed typical connective-tissue such as the substance of the cornea. The bone-corpuscles with their processes, occupying the lacunæ and canaliculi, correspond exactly to the cornea-corpuscles lying in branched spaces; while the finely fibrillated structure of the bone-lamellæ, to be presently described, resembles the fibrillated substance of the cornea in which the branching spaces lie.

Lamellæ of Compact Bone.—In the shaft of a long bone three distinct sets of lamellæ can be clearly recognised.

(1.) *General* or fundamental lamellæ; which are most easily traceable just beneath the periosteum, and around the medullary cavity, forming around the latter a series of concentric rings. At a little distance from the medullary and periosteal surfaces (in the deeper portions of the bone) they are more or less interrupted by

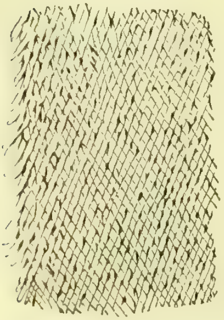


Fig. 48.—*Thin layer peeled off from a softened bone.* This figure, which is intended to represent the reticular structure of a lamella, gives a better idea of the object when held rather farther off than usual from the eye. × 400. (Sharpey.)

(2.) *Special* or Haversian lamellæ, which are concentrically arranged around the Haversian canals to the number of six to eighteen around each.

(3.) *Interstitial* lamellæ, which connect the systems of Haversian lamellæ, filling the spaces between them, and consequently attaining their greatest development where the Haversian systems are few, and *vice versâ.*

The ultimate structure of the *lamellæ* appears to be reticular. If a thin film be peeled off the surface of a bone, from which the earthy matter has been removed by acid, and examined with a high power of the microscope, it will be found composed of a finely reticular structure, formed apparently of very slender fibres decussating

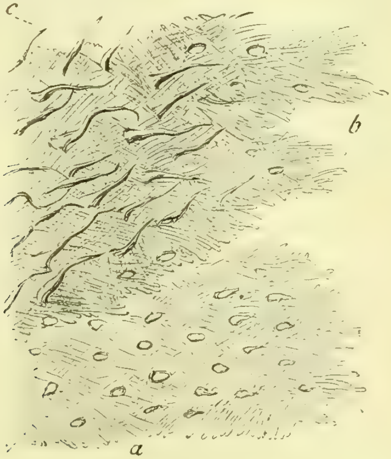


Fig. 49.—*Lamellæ torn off from a decalcified human parietal bone* at some depth from the surface. *a*, a lamella, showing reticular fibres; *b*, *b*, darker part, where several lamellæ are superposed; *c*, perforating fibres. Apertures through which perforating fibres had passed, are seen especially in the lower part, *a*, *a*, of the figure. (Allen Thomson.)

obliquely, but coalescing at the points of intersection, as if here the fibres were fused rather than woven together (fig. 48). (Sharpey.)

In many places these reticular lamellæ are perforated by tapering fibres (*Claviculi* of Gagliardi), resembling in character the ordinary white or rarely the elastic fibrous tissue, which bolt the neighbouring lamellæ together, and may be drawn out when the latter are torn asunder (fig. 49). These perforating fibres originate from ingrowing processes of the periosteum, and in the adult still retain their connection with it.

Development of Bone.—From the point of view of their development, all bones may be subdivided into two classes.

(*a.*) Those which are ossified directly in *membrane*, *e.g.*, the bones forming the vault of the skull, parietal, frontal.

(*b.*) Those whose form, previous to ossification, is laid down in *hyaline cartilage*, *e.g.*, humerus, femur.

The process of development, pure and simple, may be best studied in bones which are not preceded by cartilage—"membrane-bones" (*e.g.*, parietal); and without a knowledge of this process (ossification in *membrane*), it is impossible to understand the much more complex series of changes through which such a structure as the cartilaginous femur of the fœtus passes in its transformation into the bony femur of the adult (ossification in *cartilage*).

Ossification in Membrane.—The membrane or periosteum from which such a bone as the parietal is developed consists of two layers—an external *fibrous*, and an internal *cellular* or *osteogenetic.*

The external one consists of ordinary connective-tissue, being composed of layers of fibrous tissue with branched connective-tissue corpuscles here and there between the bundles of fibres. The internal layer consists of a network of fine fibrils with a large number of nucleated cells, some of which are oval, others drawn out into a long branched process, and others branched: it is more richly supplied with capillaries than the outer layer. The relatively large number of its cellular elements, their variability in size and shape, together with the abundance of its blood-vessels, clearly mark it out as the portion of the periosteum which is immediately concerned in the formation of bone.

In such a bone as the parietal, the deposition of bony matter, which is preceded by increased vascularity, takes place in radiating spiculæ, starting from a "centre of ossification," and shooting out in all directions towards the periphery; while the bone increases in thickness by the deposition of successive layers beneath the periosteum. The finely fibrillar network of the deeper or *osteogenetic* layer of the periosteum becomes transformed into bone-matrix (the minute structure of which has been already (p. 55) described as reticular), and its cells into bone-corpuscles. On the young bony trabeculæ thus formed, fresh layers of cells (osteoblasts) from the osteogenetic layer are developed side by side,

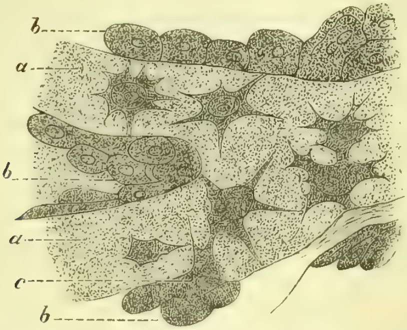


Fig. 50.—*Osteoblasts* from the parietal bone of a human embryo, thirteen weeks old. *a*, bony septa with the cells of the lacunæ; *b*, layers of osteoblasts; *c*, the latter in transition to bone corpuscles. Highly magnified. (Gegenbaur.)

lining the irregular spaces like an epithelium (fig. 50, *b*). Lime-salts are deposited in the circumferential part of each osteoblast, and thus a ring of osteoblasts gives rise to a ring of bone with the remaining uncalcified portions of the osteoblasts imbedded in it as bone-corpuscles (fig. 50).

Thus, the primitive spongy bone is formed, whose irregular branching spaces are occupied by processes from the osteogenetic layer of the periosteum with numerous blood-vessels and osteoblasts. Portions of this primitive spongy bone are re-absorbed; the osteoblasts being arranged in concentric successive layers and thus giving rise to concentric Haversian lamellæ of bone, until the irregular space in the centre is reduced to a well-formed Haversian canal, the portions of the primitive spongy bone between the Haversian systems remaining as *interstitial* or ground-lamellæ (p. 56).

The bulk of the primitive spongy bone is thus gradually converted into compact bony-tissue with Haversian canals. Those portions of the in-growths from the deeper layer of the periosteum which are not converted into bone remain in the spaces of the cancellous tissue as the red marrow.

Ossification in Cartilage.—Under this heading, taking the femur as a typical example, we may consider the process by which the solid cartilaginous rod which represents it in the fœtus is converted into the hollow cylinder of compact bone with expanded ends of cancellous tissue which forms the adult femur; bearing in mind the fact that this fœtal cartilaginous femur is many times smaller than the medullary cavity even of the shaft of the mature bone, and, therefore, that not a trace of the original cartilage can be present in the femur of the adult. Its purpose is indeed purely temporary; and, after its calcification, it is gradually and entirely re-absorbed as will be presently explained.

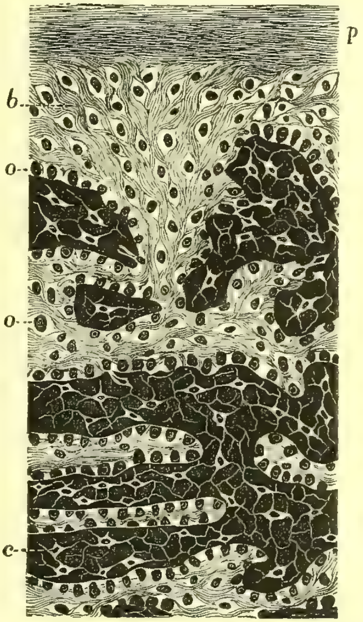


Fig. 51.—*From a transverse section through part of fœtal jaw* near the extreme periosteum, in the state of spongy bone. *p*, fibrous layer of periosteum; *b*, osteogenetic layer of periosteum; *o*, osteoblasts; *c*, osseous substance, containing many bone corpuscles. × 300. (Schofield.)

The cartilaginous rod which forms the fœtal femur is sheathed in a membrane termed the *perichondrium*, which so far resembles the periosteum described above, that it consists of two layers, in the deeper one of which spheroidal cells predominate and blood-vessels abound, while the outer layer consists mainly of fusiform cells which are in the mature tissue gradually transformed into fibres. Thus, the differences between the fœtal perichondrium and the periosteum of the adult are such as usually exist between the embryonic and mature forms of connective-tissue.

Between the hyaline cartilage of which the fœtal femur consists

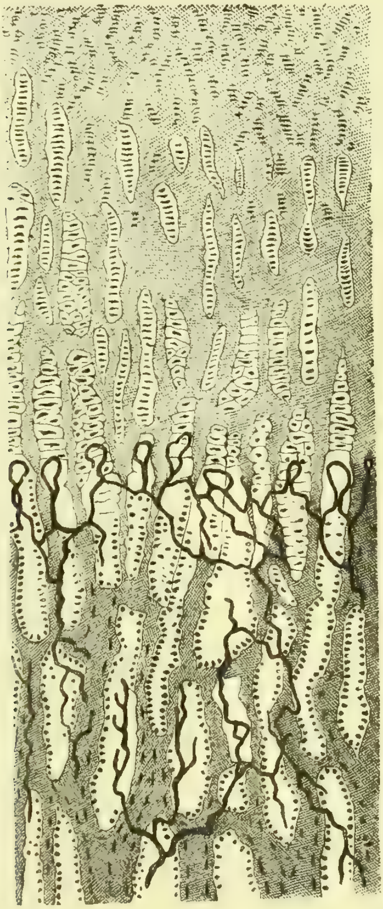


Fig. 52.—*Ossifying cartilage* showing loops of blood-vessels.

and the bony tissue forming the adult femur, two intermediate stages exist—viz., calcified cartilage, and embryonic spongy bone. These tissues, which successively occupy the place of the fœtal cartilage, are in succession entirely re-absorbed, and their place taken by true bone.

The process by which the cartilaginous is transformed into the bony femur may be divided for the sake of clearness into the following six stages :—

Stage 1.—Vascularisation of the Cartilage.— Processes from the osteogenetic or cellular layer of the perichondrium containing blood-vessels grow into the substance of the cartilage much as ivy insinuates itself into the cracks and crevices of a wall. Thus the substance of the cartilage, which previously contained no vessels, is traversed by a number of branched anastomosing channels formed by the enlargement and coalescence of the spaces in which the cartilage-cells lie, and containing loops of blood-vessels (fig. 52) and spheroidal-cells which will become osteoblasts.

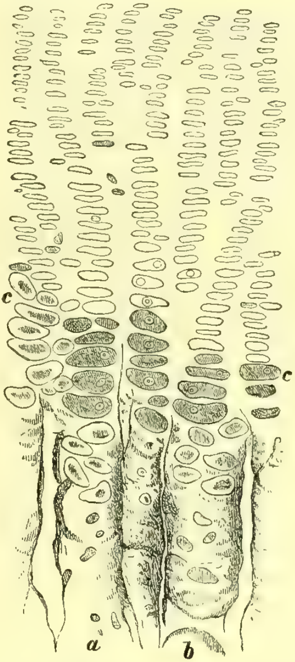


Fig. 53.—*Longitudinal section of ossifying cartilage* from the humerus of a fœtal sheep. Calcified trabeculæ are seen extending between the columns of cartilage cells. *c*, cartilage cells. × 140. (Sharpey.)

Stage 2.—Calcification of Cartilaginous Matrix.—Lime-salts are next deposited in the form of fine granules in the hyaline matrix of the cartilage, which thus becomes gradually transformed into a number of calcified trabeculæ (fig. 54, 5), forming alveolar spaces (*primary areolæ*) containing cartilage cells. By the absorption of some of the trabeculæ larger spaces arise, which contain cartilage-cells for a very short time only, their places being taken by the so-called osteogenetic layer of the perichondrium (before referred to in Stage 1) which constitutes the primary marrow. The cartilage-cells, gradually enlarging, become more transparent and finally undergo disintegration.

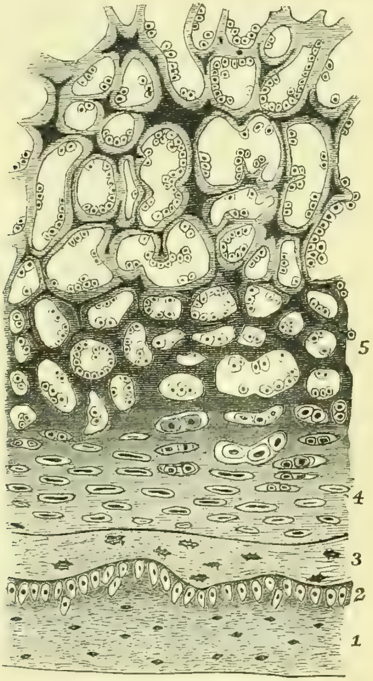


Fig. 54.—*Transverse section of a portion of a metacarpal bone of a fœtus*, showing—1, fibrous layer of periosteum; 2, osteogenetic layer of ditto; 3, periosteal bone; 4, cartilage with matrix gradually becoming calcified, as at 5, with cells in primary areolæ; beyond 5 the calcified matrix is being entirely replaced by spongy bone. × 200. (V. D. Harris.)

Stage 3.—Substitution of Embryonic Spongy Bone for Cartilage.—The cells of the primary marrow arrange themselves as a continuous layer like epithelium on the calcified trabeculæ and deposit a layer of bone, which ensheathes the calcified trabeculæ: these calcified trabeculæ, encased in their sheaths of young bone, become gradually absorbed, so that finally we have trabeculæ composed entirely of spongy bone, all trace of the original calcified cartilage having disappeared. It is probable that the large multinucleated giant-cells termed "osteoclasts" by Kölliker, which are derived from the osteoblasts by the multiplication of their nuclei, are the agents by which the absorption of calcified cartilage, and subsequently of embryonic spongy bone, is carried on (fig. 55, G). At any rate they are almost always found wherever absorption is in progress.

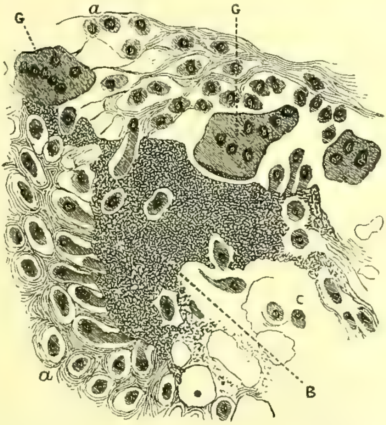


Fig. 55.—*A small isolated mass of bone* next the periosteum of the lower jaw of human fœtus. *a*, osteogenetic layer of periosteum. G, multinuclear giant cells, the one on the left acting here probably like an osteoclast. Above *c*, the osteoblasts are seen to become surrounded by an osseous matrix. (Klein and Noble Smith.)

Stages 2 and 3 are precisely similar to what goes on in the growing shaft of a bone which is increasing in length by the advance of the process of ossification into the intermediary cartilage between the diaphysis and epiphysis. In this case the cartilage-cells become flattened and, multiplying by division, are grouped into regular columns at right angles to the plane of calcification, while the process of calcification extends into the hyaline matrix between them (figs. 52 and 53).

Stage 4.—Substitution of Periosteal Bone for the Primary Embryonic Spongy Bone.—The embryonic spongy bone, formed as above described, is simply a temporary tissue occupying the place of the fœtal rod of cartilage, once representing the femur; and the stages 1, 2, and 3 show the successive changes which occur *at the centre* of the shaft. Periosteal bone is now deposited in successive layers beneath the periosteum, *i.e.*, *at the* *circumference* of the shaft, exactly as described in the section on "ossification in membrane," and thus a casing of periosteal bone is formed around the embryonic endochondral spongy bone: this casing is thickest at the centre, where it is first formed, and thins out towards each end of the shaft. The embryonic spongy bone is absorbed, its trabeculæ becoming gradually thinned and its

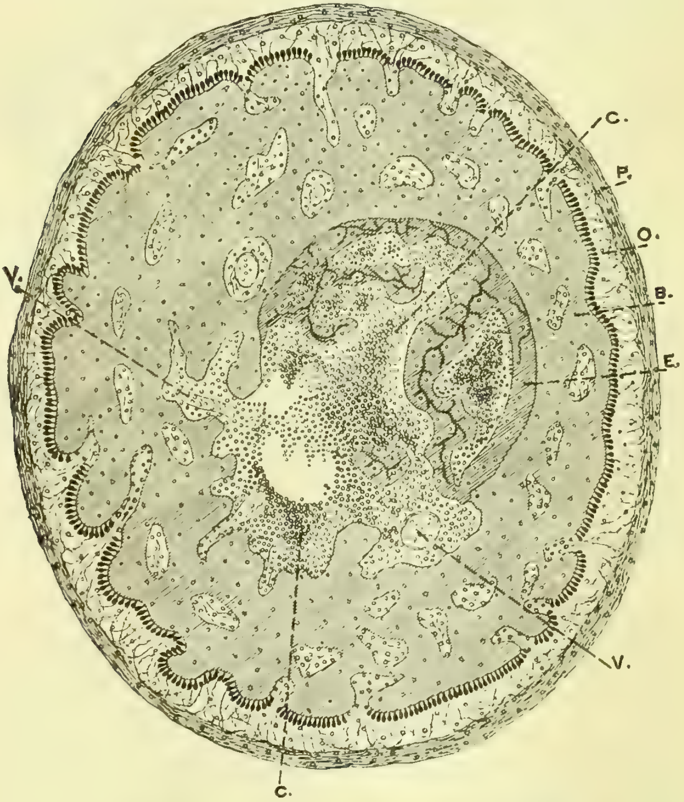


Fig. 56.—*Transverse section through the tibia of a fœtal kitten* semi-diagrammatic. × 60. P, Periosteum. O, osteogenetic layer of the periosteum, showing the osteoblasts arranged side by side, represented as pear-shaped black dots on the surface of the newly-formed bone. B, the periosteal bone deposited in successive layers beneath the periosteum and ensheathing E, the spongy endochondral bone; represented as more deeply shaded. Within the trabeculæ of endochondral spongy bone are seen the remains of the calcified cartilage trabeculæ represented as dark wavy lines. C, the medulla, with V, V, veins. In the lower half of the figure the endochondral spongy bone has been completely absorbed. (Klein and Noble Smith.)

meshes enlarging, and finally coalescing into one great cavity—the medullary cavity of the shaft.

Stage 5.—Absorption of the Inner Layers of the Periosteal Bone.—The absorption of the endochondral spongy bone is now complete, and the medullary cavity is bounded by periosteal bone: the inner layers of this periosteal bone are next absorbed, and the medullary cavity is thereby enlarged, while the deposition of bone beneath the periosteum continues as before. The first-formed periosteal bone is spongy in character.

Stage 6.—Formation of Compact Bone.—The transformation of spongy periosteal bone into compact bone is effected in a manner exactly similar to that which has been described in connection with ossification in membrane (p. 58). The irregularities in the walls of the areolæ in the spongy bone are absorbed, while the osteoblasts which line them are developed in concentric layers, each layer in turn becoming ossified till the comparatively large space in the centre is reduced to a well-formed Haversian canal (fig. 57). When once formed, bony tissue grows to some extent interstitially, as is evidenced by the fact that the lacunæ are rather further apart in fully-formed than in young bone.

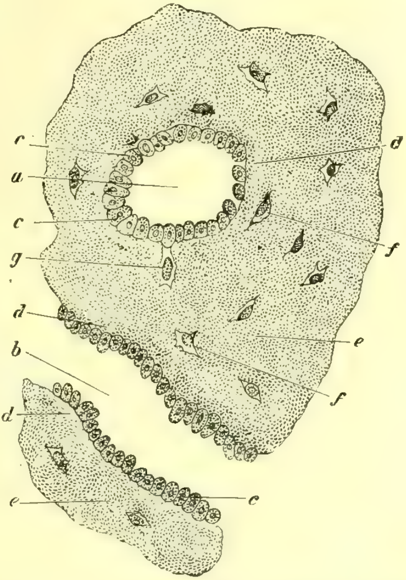


Fig. 57.—*Transverse section of femur of a human embryo* about eleven weeks old. *a*, rudimentary Haversian canal in cross section; *b*, in longitudinal section; *c*, osteoblasts; *d*, newly formed osseous substance of a lighter colour; *e*, that of greater age; *f*, lacunæ with their cells; *g*, a cell still united to an osteoblast. (Frey.)

From the foregoing description of the development of bone, it will be seen that the common terms "ossification in cartilage" and "ossification in membrane" are apt to mislead, since they seem to imply two processes radically distinct. The process of ossification, however, is in all cases one and the same, all true bony tissue being formed from membrane (perichondrium or periosteum); but in the development of such a bone as the femur, which may be taken as the type of so-called "ossification in cartilage," lime-salts are deposited in the cartilage, and this calcified cartilage is gradually and entirely re-absorbed, being ultimately replaced by bone formed from the periosteum, till in the adult structure nothing but true bone is left. Thus, in the process of "ossification in cartilage," calcification of the cartilaginous matrix precedes the real formation of bone. We must, therefore, clearly distinguish between *calcification* and *ossification.* The former is simply the infiltration of an animal tissue with lime-salts, and is, therefore, a change of chemical composition rather than of structure; while ossification is the formation of true bone—a tissue more complex and more highly organized than that from which it is derived.

Centres of Ossification.—In all bones ossification commences at one or more points, termed "centres of ossification." The long bones, *e.g.*, femur, humerus, &c., have at least three such points—one for the ossification of the *shaft* or *diaphysis*, and one for each articular extremity or *epiphysis.* Besides these three primary centres which are always present in long bones, various secondary centres may be superadded for the ossification of different *processes.*

Growth of Bone.—Bones increase *in length* by the advance of the process of ossification into the cartilage intermediate between the diaphysis and epiphysis. The increase in length indeed is due entirely to growth at the two ends of the *shaft.* This is proved by inserting two pins into the shaft of a growing bone: after some time their distance apart will be found to be unaltered though the bone has gradually increased in length, the growth having taken place beyond and not between them. If now one pin be placed in the shaft, and the other in the epiphysis, of a growing bone, their distance apart will increase as the bone grows in length.

Thus it is that if the epiphyses with the intermediate cartilage be removed from a young bone, growth in length is no longer possible; while the natural termination of growth of a bone in length takes place when the epiphyses become united in bony continuity with the shaft.

Increase *in thickness* in the shaft of a long bone, occurs by the deposition of successive layers beneath the periosteum.

If a thin metal plate be inserted beneath the periosteum of a growing bone, it will soon be covered by osseous deposit, but if it be put between the fibrous and osteogenetic layers, it will never become enveloped in bone, for all the bone is formed beneath the latter.

Other varieties of connective tissue may become ossified, *e.g.*, the tendons in some birds.

Functions of Bones.—Bones form the framework of the body; for this they are fitted by their hardness and solidity together with their comparative lightness; they serve both to protect internal organs in the trunk and skull, and as levers worked by muscles in the limbs; notwithstanding their hardness they possess a considerable degree of elasticity, which often saves them from fractures.

Teeth.

The principal part of a tooth, viz., *dentine*, is called by some a connective tissue, and on this account the structure of the teeth is considered here.

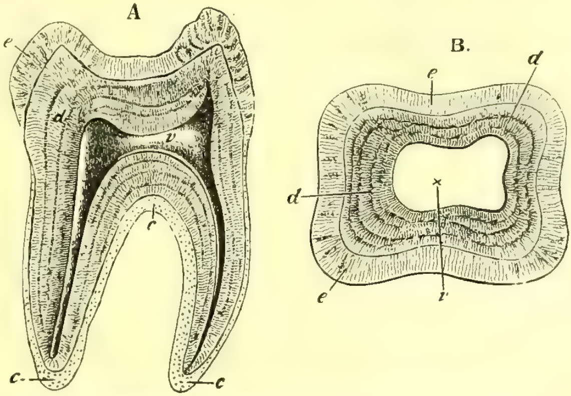


Fig. 58.—A. *Longitudinal section of a human molar tooth*; *c*, cement; *d*, dentine; *e*, enamel *v*, pulp cavity. (Owen.)
B. *Transverse section*. The letters indicate the same as in A.

A tooth is generally described as possessing a *crown*, *neck*, and *fang* or *fangs*.

The *crown* is the portion which projects beyond the level of the gum. The *neck* is that constricted portion just below the crown which is embraced by the free edges of the gum, and the *fang* includes all below this.

On making a longitudinal section through the centre of a tooth (figs. 58, 59), it is found to be principally composed of a hard matter, *dentine* or ivory; while in the centre this dentine is hollowed out into a cavity resembling in general shape the outline of the tooth, and called the *pulp* cavity, from its containing a very vascular and sensitive little mass, composed of connective-tissue, blood-vessels, and nerves, which is called the *tooth-pulp.*

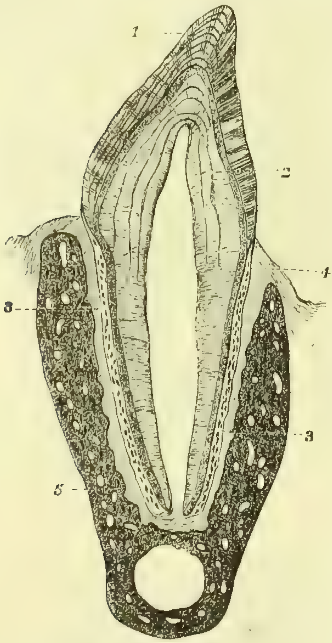


Fig. 59.—*Premolar tooth of cat in situ.* Vertical section. 1. Enamel with decussating and parallel striæ. 2. Dentine with Schreger's lines. 3. Cement. 4. Periosteum of the alveolus. 5. Inferior maxillary bone showing canal for the inferior dental nerve and vessels which appears nearly circular in transverse section. (Waldeyer.)

The blood-vessels and nerves enter the pulp through a small opening at the extremity of the fang.

Capping that part of the dentine which projects beyond the level of the gum, is a layer of very hard calcareous matter, the *enamel ;* while sheathing the portion of dentine which is beneath the level of the gum, is a layer of true bone, called the *cement* or *crusta petrosa.*

At the neck of the tooth, where the enamel and cement come into contact, each is reduced to an exceedingly thin layer. The covering of enamel becomes thicker as we approach the crown, and the cement as we approach the lower end or apex of the fang.

I.—*Dentine.*

Chemical composition.—Dentine or ivory in chemical composition closely resembles bone. It contains, however, rather less animal matter; the proportion in a hundred parts being about twenty-eight *animal* to seventy-two of *earthy*. The former, like the animal matter of bone, may be resolved into gelatin by boiling. The earthy matter is made up chiefly of calcium phosphate, with a small portion of the carbonate, and traces of calcium fluoride and magnesium phosphate.

Structure.—Under the microscope dentine is seen to be finely channelled by a multitude of delicate tubes, which, by their inner ends, communicate with the pulp-cavity, and by their outer extremities come into contact with the under part of the enamel and cement and sometimes even penetrate them for a greater or less distance (fig. 60).

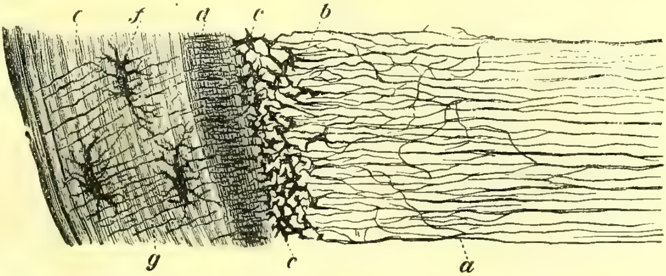


Fig. 60.—*Section of a portion of the dentine and cement from the middle of the root of an incisor tooth.* *a*, dental tubuli ramifying and terminating, some of them in the interglobular spaces *b* and *c*, which somewhat resemble bone lacunæ; *d*, inner layer of the cement with numerous closely set canaliculi; *e*, outer layer of cement; *f*, lacunæ; *g*, canaliculi. × 350. (Kölliker.)

In their course from the pulp-cavity to the surface of the dentine, the minute tubes form gentle and nearly parallel curves and divide and subdivide dichotomously, but without much lessening of their calibre until they are approaching their peripheral termination.

From their sides proceed other exceedingly minute secondary canals, which extend into the dentine between the tubules, and anastomose with each other. The tubules of the dentine, the average diameter of which at their inner and larger extremity is $\frac{1}{4500}$ of an inch, contain fine prolongations from the tooth-pulp, which give the dentine a certain faint sensitiveness under ordinary circumstances and, without doubt, have to do also with its nutrition. These prolongations from the tooth-pulp are really processes of the dentine-cells or *odontoblasts* which are branched cells lining the pulp-cavity; the relation of these processes to the tubules in which they lie being precisely similar to that of the processes of the bone-corpuscles to the canaliculi of bone. The outer portion of the dentine, underlying both the cement and enamel, forms a more or less distinct layer termed the *granular* or *interglobular* layer. It is characterised by the presence of a number of minute cell-like cavities, much more closely packed than the lacunæ in the cement, and communicating with one another and with the ends of the dentine-tubes (fig. 60), and containing cells like bone-corpuscles.

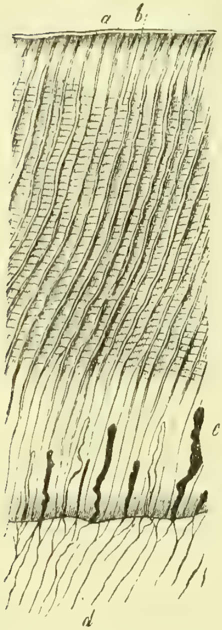


Fig. 61. — *Thin section of the enamel and a part of the dentine.* *a*, cuticular pellicle of the enamel; *b*, enamel fibres, or columns with fissures between them and cross striæ; *c*, larger cavities in the enamel, communicating with the extremities of some of the tubuli (*d*). × 350. (Kölliker.)

II.—*Enamel.*

Chemical composition.—The *enamel*, which is by far the hardest portion of a tooth, is composed, chemically, of the same elements that enter into the composition of dentine and bone. Its animal matter, however, amounts only to about 2 or 3 per cent. It contains a larger proportion of inorganic matter and is harder than any other tissue in the body.

Structure. — Examined under the microscope, enamel is found composed of fine hexagonal fibres (figs. 61, 62) $\frac{1}{5000}$ of an inch in diameter, which are set on end on the surface of the dentine, and fit into corresponding depressions in the same.

They radiate in such a manner from the dentine that at the top of the tooth they are more or less vertical, while towards the sides they tend to the horizontal direction. Like the dentine tubules, they are not straight, but disposed in wavy and parallel curves. The fibres are marked by transverse lines, and are mostly solid, but some of them contain a very minute canal.

The enamel-prisms are connected together by a very minute quantity of hyaline cement-substance. In the deeper part of the enamel, between the prisms, are small *lacunæ*, which communicate with the "interglobular spaces" on the surface of the dentine.

The enamel itself is coated on the outside by a very thin calcified membrane, sometimes termed the *cuticle* of the enamel.

III.—*Crusta Petrosa.*

The *crusta petrosa*, or *cement* (fig. 60, *c*, *d*), is composed of true bone, and in it are lacunæ (*f*) and canaliculi (*g*) which sometimes communicate with the outer finely branched ends of the dentine tubules. Its laminæ are as it were bolted together by perforating fibres like those of ordinary bone, but it differs in possessing Haversian canals only in the thickest part.

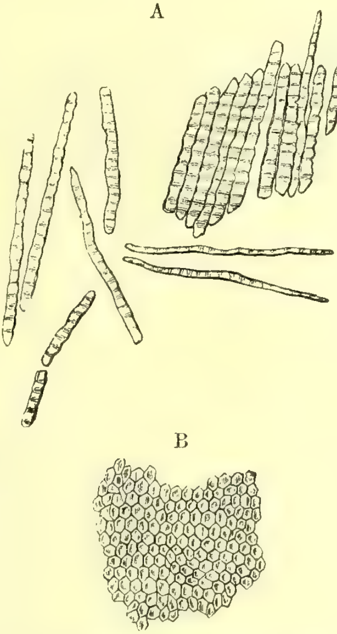


Fig. 62.—*Enamel fibres.* A, fragments and single fibres of the enamel, isolated by the action of hydrochloric acid. B, surface of a small fragment of enamel, showing the hexagonal ends of the fibres. × 350. (Kölliker.)

Development of Teeth.

Development of the Teeth.—The first step in the development of the teeth consists in a downward growth (fig. 63, A, 1) from the stratified epithelium of the mucous membrane of the mouth, now thickened in the neighbourhood of the maxillæ which are in the course of formation. This process passes downward into a recess (enamel groove) of the imperfectly developed tissue of which the chief part of the jaw consists. The downward epithelial growth forms the *primary enamel organ* or *enamel germ*, and its position is indicated by a slight groove in the mucous membrane of the jaw.

The next step in the process consists in the elongation downward of the enamel groove and of the enamel germ and the inclination outward of the deeper part (fig. 63, B, *f′*), which is now inclined at an angle with the upper portion or neck (*f*), and has become bulbous. After this, there is an increased development at certain points corresponding to the situations of the future milk teeth, and the enamel germ, or common enamel germ, as it may be called, becomes divided at its deeper portion, or extended by

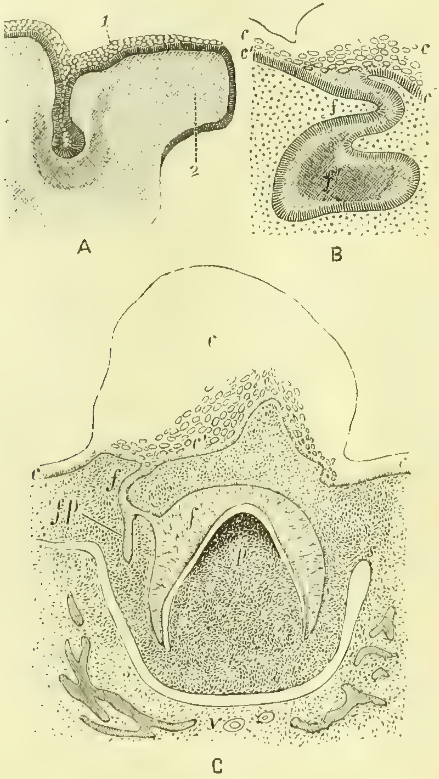


Fig. 63.—*Section of the upper jaw of a fœtal sheep.* A.—1, common enamel-germ dipping down into the mucous membrane; 2, palatine process of jaw. B.—Section similar to A, but passing through one of the special enamel-germs here becoming flask-shaped; *c*, *c′*, epithelium of mouth; *f*, neck; *f′*, body of special enamel-germ. C.—A later stage; *c*, outline of epithelium of gum; *f*, neck of enamel-germ; *f′*, enamel organ; *p*, papilla; *s*, dental sac forming; *f p*, the enamel-germ of permanent tooth. (Waldeyer and Kölliker.) Copied from Quain's Anatomy.

further growth, into a number of special enamel germs corresponding to each of the above-mentioned milk teeth, and connected to the common germ by a narrow neck, each tooth being placed in its own special recess in the embryonic jaw (fig. 63, B, *f f'*).

As these changes proceed, there grows up from the underlying tissue into each enamel germ (fig. 63, C, *p*), a distinct vascular *papilla* (dental papilla), and upon it the enamel germ becomes moulded and presents the appearance of a cap of two layers of epithelium separated by an interval (fig. 63, C, *f'*). Whilst part of the sub-epithelial tissue is elevated to form the dental papillæ, the part which bounds the embryonic teeth forms the dental sacs (fig. 63, C, *s*); and the rudiment of the jaw, at first a bony gutter in which the teeth germs lie, sends up processes forming partitions between the teeth. In this way small chambers are produced in which the dental sacs are contained, and thus the sockets of the teeth are formed. The papilla, which is really part of the dental sac, if one thinks of this as the whole of the sub-epithelial tissue surrounding the enamel organ and interposed between the enamel germ and the developing bony jaw, is composed of nucleated cells arranged in a meshwork, the outer or peripheral part being covered with a layer of columnar nucleated cells called *odontoblasts*. The odontoblasts form the dentine, while the remainder of the papilla forms the tooth-pulp. The method of the formation of the dentine from the odontoblasts is as follows:—The cells elongate at their outer part, and these processes are directly converted into the tubules of dentine (fig. 64).

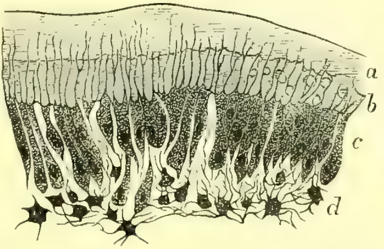


Fig. 64.—*Part of section of developing tooth of a young rat*, showing the mode of deposition of the dentine. Highly magnified. *a*, outer layer of fully formed dentine; *b*, uncalcified matrix with one or two nodules of calcareous matter near the calcified parts; *c*, odontoblasts sending processes into the dentine; *d*, pulp. The section is stained in carmine, which colours the uncalcified matrix but not the calcified part. (E. A. Schäfer.)

The continued formation of dentine proceeds by the elongation of the odontoblasts, and their subsequent conversion by a process of calcification into dentine tubules. The most recently formed tubules are not immediately calcified. The dentine fibres contained in the tubules are said to be formed from processes of the deeper layer of odontoblasts, which are wedged in between the cells of the superficial layer (fig. 64) which form the tubules only.

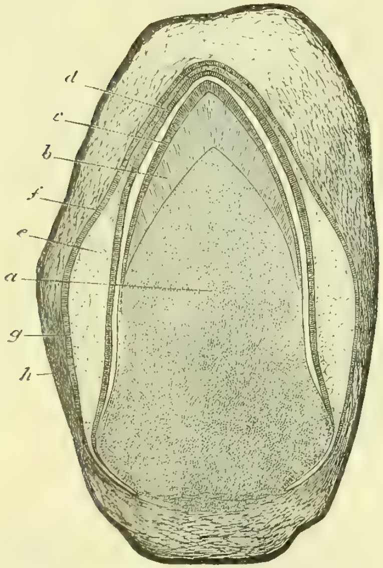


Fig. 65.—*Vertical transverse section of the dental sac, pulp, &c.*, of a kitten. *a*, dental papilla or pulp; *b*, the cap of dentine formed upon the summit; *c*, its covering of enamel; *d*, inner layer of epithelium of the enamel organ; *e*, gelatinous tissue; *f*, outer epithelial layer of the enamel organ; *g*, inner layer, and *h*, outer layer of dental sac. × 14. (Thiersch.)

Since the papillæ are to form the main portion of each tooth, *i.e.*, the dentine, each of them early takes the shape of the crown of the tooth it is to form. As the dentine increases in thickness, the papillæ diminish, and at last when the tooth is cut, only a small amount of the papilla remains as the dental pulp, and is supplied by vessels and nerves which enter at the end of the fang. The shape of the crown of the tooth is taken by the corresponding papilla, and that of the single or double fang by the subsequent constriction below the crown, or by division of the lower part of the papilla.

The enamel cap is found later on to consist (fig. 65) of three parts: (*a*) an inner membrane, composed of a layer of columnar epithelium in contact with the dentine, called *enamel cells*, and outside of these one or more layers of small polyhedral nucleated cells (*stratum intermedium* of Hannover); (*b*) an outer membrane of several layers of epithelium; (*c*) a middle membrane formed of a matrix of non-vascular, gelatinous tissue, containing a hyaline interstitial substance. The enamel is formed by the enamel cells of the inner membrane, by the elongation of their distal extremities, and the direct conversion of these processes into enamel. The calcification of the enamel processes or prisms takes place first at the periphery, the centre remaining for a time transparent. The cells of the stratum intermedium are used for the regeneration of the enamel cells, but these and the middle membrane after a time disappear. The cells of the outer membrane give origin to the cuticle of the enamel.

The *cement* or *crusta petrosa* is formed from the tissue of the tooth sac, the structure and function of which are identical with those of the osteogenetic layer of the periosteum.

In this manner the first set of teeth, or the milk-teeth, are formed ; and each tooth, by degrees developing, presses at length on the wall of the sac enclosing it and, causing its absorption, is *cut*, to use a familiar phrase.

The *temporary* or *milk-teeth* have only a very limited term of existence. This is due to the growth of the permanent teeth, which push their way up from beneath, absorbing in their progress the whole of the fang of each milk-tooth and leaving at length only the crown as a mere shell, which is shed to make way for the eruption of the permanent teeth (fig. 66).

The temporary teeth are ten in each jaw, namely, four *incisors*, two *canines*, and four *molars*, and are replaced by ten permanent teeth, each of which is developed in a way almost exactly similar to the manner of development already described, from a small process or sac set by, so to speak, from the enamel germ of the temporary tooth which precedes it, and called the *cavity of reserve*.

The number of permanent teeth in each jaw is, however, increased to sixteen, by the development of three others on each side of the jaw after much the same fashion as that by which the milk-teeth were themselves formed.

The beginning of the development of the permanent teeth of course takes place long before the *cutting* of those which they are to succeed. One of the first steps in the development of a milk-tooth is the outgrowth of a lateral process of epithelial cells from its primitive enamel organ (fig. 63, c, *f p*). This epithelial outgrowth ultimately becomes the enamel organ of the permanent tooth, and is indented from below by a primitive dental papilla, precisely as described above.

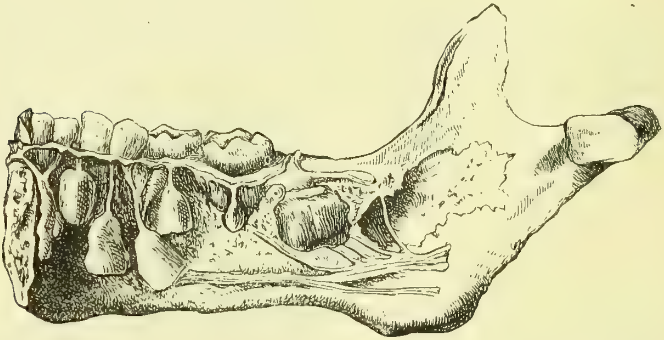


Fig. 66.—*Part of the lower jaw of a child* of three or four years old, showing the relations of the temporary and permanent teeth. The specimen contains all the milk-teeth of the right-side, together with the incisors of the left; the inner plate of the jaw has been removed, so as to expose the sacs of all the permanent teeth of the right side, except the eighth or wisdom tooth, which is not yet formed. The large sac near the ascending ramus of the jaw is that of the first permanent molar, and above and behind it is the commencing rudiment of the second molar. (Quain.)

The following formula shows, at a glance, the comparative arrangement and number of the temporary and permanent teeth :—

		MO.	CA.	IN.	CA.	MO.		
Temporary Teeth	Upper	2	1	4	1	2	= 10	= 20
	Lower	2	1	4	1	2	= 10	

		MO.	BI.	CA.	IN.	CA.	BI.	MO.		
Permanent teeth	Upper	3	2	1	4	1	2	3	= 16	= 32
	Lower	3	2	1	4	1	2	3	= 16	

From this formula it will be seen that the two bicuspid teeth in the adult are the successors of the two molars in the child. They differ from them, however, in some respects, the *temporary* molars having a stronger likeness to the *permanent* than to their immediate descendants, the so-called bicuspids.

The temporary incisors and canines differ from their successors but little except in their smaller size.

The following tables show the average times of eruption of the Temporary and Permanent teeth. In both cases, the eruption of any given tooth of the lower jaw precedes, as a rule, that of the corresponding tooth of the upper.

Temporary or Milk Teeth.

The figures indicate in *months* the age at which each tooth appears.

MOLARS.	CANINES.	INCISORS.	CANINES.	MOLARS.
24 12	18	9 7 7 9	18	12 24

Permanent Teeth.

The age at which each tooth is cut is indicated in this table in *years.*

MOLARS.	BICUSPID.	CANINES.	INCISORS.	CANINES.	BICUSPID.	MOLARS.
17 to 25 12 to 13 6	10 9	11 to 12	8 7 7 8	11 to 12	9 10	6 12 to 13 17 to 25

The times of eruption put down in the above tables are only approximate: the limits of variation being tolerably wide. Some children may cut their first teeth before the age of six months and others not till nearly the twelfth month. In nearly all cases the two central incisors of the lower jaw are cut first; these being succeeded after a short interval by the four incisors of the upper jaw, next follow the lateral incisors of the lower jaw, and so on as indicated in the table till the completion of the milk dentition at about the age of two years.

The milk-teeth usually come through in batches, each period of eruption being succeeded by one of quiescence lasting sometimes several months. The milk-teeth are in use from the age of two up to five and a half years: at about this age the first permanent molars (four in number) make their appearance *behind* the milk-molars, and for a short time the child has four permanent and twenty temporary teeth in position at once.

It is worthy of note that from the age of five years to the shedding of the first milk-tooth the child has no fewer than forty-eight teeth, twenty milk-teeth and twenty-eight calcified germs of permanent teeth (all in fact except the four wisdom teeth).

CHAPTER IV.

THE BLOOD.

THE blood of man, as indeed of the great majority of vertebrate animals, is a more or less viscid fluid, of a red colour. The exact shade of red is variable, for whereas that taken from the arteries, from the left side of the heart or from the pulmonary veins, is of a bright scarlet hue, that obtained from the systemic veins, from the right side of the heart, or from the pulmonary artery, is of a much darker colour, and varies from bluish-red to reddish-black. To the naked eye, the red colour appears to belong to the whole mass of blood, but on examination with the microscope it is found that this is not the case. By the aid of this instrument the blood is shown to consist in reality of an almost colourless fluid, called *Liquor Sanguinis* or *Plasma*, in which are suspended numerous minute rounded masses of protoplasm, called *Blood Corpuscles.* The corpuscles are, for the most part, coloured, and it is to their presence that the red colour of the blood is due.

Even when examined in very thin layers blood is *opaque*, on account of the different refractive powers possessed by its two constituents, viz., the plasma and the corpuscles. On treatment with chloroform and other reagents, however, it becomes transparent, and assumes a lake colour, in consequence of the colouring matter of the corpuscles having been, by these means, discharged into the plasma. The average *specific gravity* of blood at 60° F. (15° C.) is 1055, the extremes consistent with health being 1045-1062. The *reaction* of blood is faintly alkaline. Its *temperature* varies within narrow limits, the average being 100° F. (37·8° C.). The blood stream is slightly warmed by passing through the muscles, nerve centres, and glands, but is somewhat cooled on traversing the capillaries of the skin. Recently drawn blood has a distinct *odour*, which in many cases is characteristic of the animal from which it has been taken ; the odour may be further developed by adding to blood a mixture of equal parts of sulphuric acid and water.

Quantity of the Blood.—The quantity of blood in any animal under normal conditions bears a pretty constant relation to the body weight. The methods employed for estimating it are not so simple as might at first sight be thought. For example, it would not be possible to get any accurate information on the point from the amount obtained by rapidly bleeding an animal to death, for then an indefinite quantity would remain in the vessels, as well as in the tissues; nor, on the other hand, would it be possible to obtain a correct estimate by less rapid bleeding, as, since life would be more prolonged, time would be allowed for the passage into the blood of lymph from the lymphatic vessels and from the tissues. In the former case, therefore, we should under-estimate, and in the latter over-estimate the total amount of the blood.

Of the several methods which have been employed, the most accurate appears to be the following. A small quantity of blood is taken from an animal by venesection; it is defibrinated and measured, and used to make standard solutions of blood. The animal is then rapidly bled to death, and the blood which escapes is collected. The blood vessels are next washed out with water or saline solution until the washings are no longer coloured, and these are added to the previously withdrawn blood; lastly the whole animal is finely minced with water or saline solution. The fluid obtained from the mincings is carefully filtered, and added to the diluted blood previously obtained, and the whole is measured. The next step in the process is the comparison of the colour of the diluted blood with that of standard solutions of blood and water of a known strength, until it is discovered to what standard solution the diluted blood corresponds. As the amount of blood in the corresponding standard solution is known, as well as the total quantity of diluted blood obtained from the animal, it is easy to calculate the absolute amount of blood which the latter contained, and to this is added the small amount which was withdrawn to make the standard solutions. This gives the total amount of blood which the animal contained. It is contrasted with the weight of the animal, previously known. The result of many experiments shows that the quantity of blood in various animals averages $\frac{1}{12}$ to $\frac{1}{14}$ of the total body weight.

An estimate of the quantity in man which corresponded nearly with the above, was made some years ago from the following data. A criminal was weighed before and after decapitation; the difference in the weight representing, of course, the quantity of blood which escaped. The blood-vessels of the head and trunk were then washed out by the injection of water, until the fluid which escaped had only a pale red or straw colour. This fluid was then also weighed; and the amount of blood which it represented was calculated by comparing the proportion of solid matter contained in it with that of the first blood which escaped on decapitation. Two experiments of this kind gave precisely similar results. (Weber and Lehmann.)

It should be remembered, however, in connection with these estimations, that the quantity of the blood must vary, even in the same animal, very considerably with the amount of both the ingesta and egesta of the period immediately preceding the experiment; and it has been found, indeed, that the quantity of blood obtainable from a fasting animal barely exceeds a half of that which is present soon after a full meal.

Coagulation of the Blood.—One of the most characteristic properties which the blood possesses is that of *clotting* or *coagulating*, when removed from the body. This phenomenon may be observed under the most favourable conditions in blood which has been drawn into an open vessel. In about two or three minutes, at the ordinary temperature of the air, the surface of the fluid is seen to become semi-solid or jelly-like; this change next taking place, in a minute or two, at the sides of the vessel in which it is contained, and then extending throughout the entire mass.

The time which is required for the blood to become solid is about eight or nine minutes. The solid mass occupies exactly the same volume as the previously liquid blood, and adheres so closely to the sides of the containing vessel that if it be inverted none of its contents escape. The solid mass is the *crassamentum* or *clot*. If the clot be watched for a few minutes, drops of a light, straw-coloured fluid, the *serum*, may be seen to make their appearance on the surface and, as they become more and more numerous, run together, forming a complete superficial stratum above the solid clot. At the same time the fluid begins to transude at the sides and at the under surface of the clot, which in the course of an hour or two floats in the liquid. The first drops of serum appear on the surface about eleven or twelve minutes after the blood has been drawn; and the fluid continues to transude for from thirty-six to forty-eight hours.

The clotting of blood is due to the development in it of a substance called *fibrin*, which appears as a meshwork (fig. 67) of fine fibrils. This meshwork entangles and encloses within it the blood corpuscles, as clotting takes place too quickly to allow them to sink to the bottom of the plasma. The first clot formed, therefore, includes the whole of the constituents of the blood in an apparently solid mass, but soon the fibrinous meshwork begins to contract, and the serum which does not belong to the clot is squeezed out. When the whole of the serum has transuded, the clot is found to be smaller, but firmer and harder, as it is now made up of fibrin and blood corpuscles only. It will be noticed that coagulation rearranges the constituents of the blood according to the following scheme, liquid blood being made up of plasma and blood-corpuscles, and clotted blood of serum and clot.

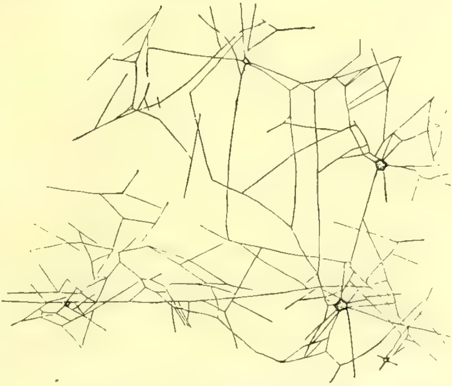
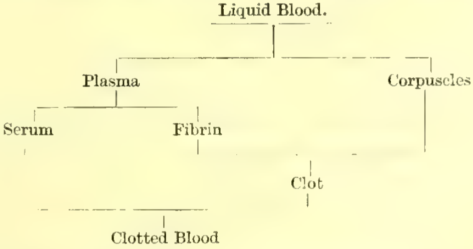


Fig. 67.—*Reticulum of fibrin*, from a drop of human blood, after treatment with rosanilin. (Ranvier.)



Buffy Coat.—Under ordinary circumstances coagulation occurs, as we have mentioned above, before the red corpuscles have had time to subside; and thus from their being entangled in the meshes of the fibrin, the clot is of a deep red colour throughout, somewhat darker, it may be, at the most dependent part, from accumulation of red corpuscles, but not to any very marked degree. When, however, coagulation is delayed from any cause, as when blood is kept at a temperature of 32° F. (0° C.), or when clotting is normally a slow process, as in the case of horse's blood, or, lastly, in certain diseased conditions of the blood in which clotting is naturally delayed, time is allowed for the coloured corpuscles to sink to the bottom of the fluid. When clotting does occur, the upper layers of the blood, being free of coloured corpuscles and consisting chiefly of fibrin, form a superficial stratum differing in appearance from the rest of the clot, in that it is of a grayish yellow colour. This is known as the "*buffy coat.*"

Cupped appearance of the Clot.—When the buffy coat has been produced in the manner just described, it commonly contracts more than the rest of the clot, on account of the absence of coloured corpuscles from its meshes, and because contraction is less interfered with by adhesion to the interior of the containing vessel in the vertical than the horizontal direction. This produces a cup-like appearance of the buffy coat, and the clot is not only buffed but cupped on the surface. The buffed and cupped appearance of the clot is well marked in certain states of the system, especially in inflammation, where the fibrin-forming constituents are in excess, and it is also well marked in chlorosis where the corpuscles are deficient in quantity.

Formation of Fibrin.—In describing the coagulation of the blood in the preceding paragraphs, it was stated that this phenomenon was due to the development in the clotting blood of a meshwork of fibrin. This may be demonstrated by taking recently-drawn blood, and whipping it with a bundle of twigs; the fibrin is found to adhere to the twigs as a reddish-white, stringy mass, having been thus obtained from the fluid nearly free from coloured corpuscles. The defibrinated blood no longer retains the power of spontaneous coagulability.

The fibrin which makes its appearance in the blood when it is undergoing coagulation is derived chiefly, if not entirely, from the plasma or liquor sanguinis; for although the colourless corpuscles are intimately connected with the process in a way which will be presently explained, the coloured corpuscles appear to take no active part in it whatever. This may be shown by experimenting with plasma free from coloured corpuscles. Such plasma may be procured by delaying coagulation in blood, by keeping it at a low temperature, 32° F. (0° C.), until the coloured corpuscles which are of higher specific gravity than the other constituents of blood, have had time to sink to the bottom of the containing vessel, and to leave an upper stratum of colourless plasma, in the lower layers of which are many colourless corpuscles. The blood of the horse is specially suited for the purposes of this experiment; and the upper stratum of colourless plasma derived from it, if decanted into another vessel and exposed to the ordinary temperature of the air, will coagulate just as though it were the entire blood, producing a clot similar in all respects to blood clot, except that it is almost colourless from the absence of red corpuscles. If some of the plasma be diluted with *neutral saline solution, coagulation is delayed, and the stages of the gradual formation of fibrin may be more conveniently watched. The viscidity which precedes the complete coagulation may be seen to be due to fibrin fibrils developing in the fluid—first of all at the circumference of the containing vessel, and gradually extending throughout the mass. Again, if plasma be whipped with a bundle of twigs, the fibrin may be obtained as a solid, stringy mass, just in the same way as from the entire blood, and the resulting fluid no longer retains its power of spontaneous coagulability. Evidently, therefore, fibrin is derived from the plasma and not from the coloured corpuscles. In these experiments, it is not necessary that the plasma shall have been obtained by the process of cooling above described, as plasma obtained in any other way, *e.g.*, by allowing blood to flow direct from the vessels of an animal into a vessel containing a third or a fourth of the bulk of the blood of a saturated solution of a neutral salt (preferably of magnesium sulphate) and mixing carefully, will answer the purpose and, just as in the other case the coloured corpuscles will subside leaving the clear superstratum of

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* Neutral saline solution commonly consists of a ·75 solution of common salt (sodium chloride) in water.

(salted) plasma. In order to cause this plasma to coagulate, it is necessary to get rid of the salts by dialysis, or to dilute it with several times its bulk of water.

The antecedent of Fibrin.—If plasma be saturated with *solid* magnesium sulphate or sodium chloride, a white, sticky, precipitate called *plasmine* is thrown down, after the removal of which, by filtration, the plasma will not spontaneously coagulate. This *plasmine* is soluble in dilute neutral saline solutions, and the solution of it speedily coagulates, producing a clot composed of fibrin. From this we see that blood plasma contains a substance without which it cannot coagulate, and a solution of which is spontaneously coagulable. This substance is very soluble in dilute saline solutions, and is not, therefore, fibrin, which is insoluble in these fluids. We are, therefore, led to the belief that plasmine produces or is converted into fibrin, when clotting of fluids containing it takes place.

Nature of Plasmine.—There seems distinct evidence that plasmine is a compound body made up of two or more substances, and that it is not mere soluble fibrin. This view is based upon the following observations:—There exists in all the serous cavities of the body in health, *e.g.*, the pericardium, the peritoneum, and the pleura, a certain small amount of transparent fluid, generally of a pale straw colour, which in diseased conditions may be greatly increased. It somewhat resembles serum in appearance, but in reality differs from it, and is probably identical with plasma. This serous fluid is not, as a rule, spontaneously coagulable, but may be made to clot on the addition of serum, which is also a fluid which has no tendency of itself to coagulate. The clot produced consists of fibrin, and the clotting is identical with the clotting of plasma. From the serous fluid (that from the inflamed *tunica vaginalis testis* or *hydrocele* fluid is mostly used) we may obtain, by saturating it with *solid* magnesium sulphate or sodium chloride, a white viscid substance as a precipitate which is called *fibrinogen*, which may be separated by filtration, and is then capable of being dissolved in water, as a certain amount of the neutral salt is entangled with the precipitate sufficient to produce a dilute saline solution in which it is soluble. This body belongs to the *globulin* class of proteid substances. Its solution has no tendency to clot of itself. Fibrinogen may also be obtained as a viscid precipitate from hydrocele fluid by diluting it with water, and passing a brisk stream of carbon dioxide gas through the solution. Now if serum be added to a solution of fibrinogen, the mixture clots.

From serum may be obtained another globulin very similar in properties to fibrinogen, if it be subjected to treatment similar to either of the two methods by which fibrinogen is obtained from hydrocele fluid ; this substance is called *paraglobulin*, and it may be separated by filtration and dissolved in a dilute saline solution in a manner similar to fibrinogen.

If the solutions of fibrinogen and paraglobulin be mixed, the mixture cannot be distinguished from a solution of plasmine, and like that solution (in a great majority of cases) firmly clots whereas a mixture of the hydrocele fluid and serum, from which they have been respectively taken, no longer does so. In addition to this evidence of the compound nature of plasmine, it may be further shown that, if sufficient care be taken, both fibrinogen and paraglobulin may be obtained from plasma : fibrinogen, as a flaky precipitate, by adding carefully 13 per cent. of crystalline sodium chloride ; and after the removal of fibrinogen from the plasma by filtration, paraglobulin may be afterwards precipitated, on th further addition of the same salt or of magnesium sulphate to the filtrate. It is evident, therefore, that both these substances must be thrown down together when plasma is saturated with sodium chloride or magnesium sulphate, and that the mixture of the two corresponds with plasmine.

Presence of a Fibrin Ferment.—So far it has been shown that *plasmine*, the antecedent of fibrin in blood, to the possession of which blood owes its power of coagulating, is not a simple body, but is composed of at least two factors—viz., fibrinogen and paraglobulin ; there is reason for believing that yet another body is associated with them in plasmine to produce coagulation ; this is what is known under the name of *fibrin ferment* (Schmidt). It was at one time thought that the reason why hydrocele fluid coagulated when serum was added to it was that the latter fluid supplied the paraglobulin which the former lacked ; this, however, is not the case, as hydrocele does not lack this body, and if paraglobulin, obtained from serum by the carbonic acid method, be added to it, it will not coagulate, neither will a mixture of solutions of fibrinogen and paraglobulin obtained in the same way. But if paraglobulin, obtained by the saturation method, be added to hydrocele fluid, it will clot, as will also, as we have seen above, a mixed solution of fibrinogen and paraglobulin, when obtained by the saturation method. From this it is evident that in plasmine there is something more than the two bodies above mentioned, and that this something is precipitated with the paraglobulin by the saturation method, and is not precipitated by the carbonic acid method. The following experiments show that it is of the nature of a ferment. If defibrinated blood or serum be kept in a stoppered bottle with its own bulk of alcohol for some weeks, all the proteid matter is precipitated in a coagulated form; if the precipitate be then removed by filtration, dried over sulphuric acid, finely powdered, and then suspended in water, a watery extract may be obtained by further filtration, containing extremely little, if any, proteid matter. Yet a little of this watery extract will determine coagulation in fluids, *e.g.*, hydrocele fluid or diluted plasma, which are not spontaneously coagulable, or which coagulate slowly and with difficulty. It will also cause a mixture of fibrinogen and paraglobulin, obtained by the carbonic acid method, to clot. This watery extract appears to contain the body which is precipitated with the paraglobulin by the saturation method. Its active properties are entirely destroyed by boiling. The amount of the extract added does not influence the amount of the clot formed, but only the rapidity of clotting, and moreover the active substance contained in the extract evidently does not form part of the clot, as it may be obtained from the serum after blood has clotted. So that the third factor, which is contained in the aqueous extract of blood, belongs to that class of bodies which promote the union of other bodies, or cause changes in other bodies, without themselves entering into union or undergoing change, *i.e. ferments.* The third substance has, therefore, received the name *fibrin ferment.* This ferment is developed in blood soon after it has been shed, and its amount appears to increase for a certain time afterwards (p. 92).

The part played by Paraglobulin.—So far we have seen that plasmine is a body composed of three substances, viz., fibrinogen, paraglobulin, and fibrin ferment. The question presents itself, are these three bodies actively concerned in the formation of fibrin?

Here we come to a point about which two distinct opinions prevail, and which it will be necessary to mention. Schmidt holds that fibrin is produced by the interaction of the two proteid bodies, viz., fibrinogen and paraglobulin, brought about by the presence of a special fibrin ferment. Also, that when coagulation does not occur in serum, which contains paraglobulin and the fibrin ferment, the non-coagulation is accounted for by lack of fibrinogen, and when it does not occur in fluids which contain fibrinogen, it is due to the absence of paraglobulin, or of the ferment, or of both. It will be seen that, according to this view, paraglobulin has a very important fibrino-plastic property. The other opinion, held by Hammersten, is that paraglobulin is not an essential in coagulation, or at any rate does not take an active part in the process. He believes that paraglobulin possesses the property in common with many other bodies of combining with—or decomposing, and so rendering inert—certain substances which have the power of preventing the formation or precipitation of fibrin, this power of preventing coagulation being well known to belong to the free alkalies, to the alkaline carbonates, and to certain salts; and he looks upon fibrin as formed from fibrinogen, which is either (1) decomposed into that substance with the production of some other substances; or (2) bodily converted into it under the action of a ferment, which is frequently precipitated with paraglobulin.

Influence of Salts on Coagulation.—It is believed that the presence of a certain but small amount of salts, especially of sodium chloride, is necessary for coagulation, and that without it, clotting cannot take place.

Sources of the Fibrin Generators.—It has been previously remarked that the colourless corpuscles which are always present in smaller or greater numbers in the plasma, even when this has been freed from coloured corpuscles, have an important share in the production of the clot. The proofs of this may be briefly summarised as follows:—(1) That all strongly coagulable fluids contain colourless corpuscles almost in direct proportion to their coagulability; (2) That clots formed on foreign bodies, such as needles inserted into the interior of living blood-vessels, are preceded by an aggregation of colourless corpuscles; (3) That plasma in which the colourless corpuscles happen to be scanty, clots feebly; (4) That if horse's blood be kept in the cold, so that the corpuscles subside, it will be found that the lowest stratum, containing chiefly coloured corpuscles, will, if removed, clot feebly, as it contains little of the fibrin factors; whereas the colourless plasma, especially the lower layers of it in which the colourless corpuscles are most numerous, will clot well, but if filtered in the cold will not clot so well, indicating that when filtered nearly free from colourless corpuscles even the plasma does not contain sufficient of all the fibrin factors to produce thorough coagulation; (5) In a drop of coagulating blood, observed under the microscope, the fibrin fibrils are seen to start from the colourless corpuscles.

Although the intimate connection of the colourless corpuscles with the process of coagulation seems indubitable, for the reasons just given, the exact share which they have in contributing the various fibrin factors remains still uncertain. It is generally believed that the fibrin-ferment at any rate is contributed by them, inasmuch as the quantity of this substance obtainable from plasma bears a direct relation to the numbers of colourless corpuscles which the plasma contains. Many believe that the fibrinogen also is wholly or in part derived from them.

Conditions affecting Coagulation.—The coagulation of the blood is **hastened** by the following means:—

1. **Moderate warmth,**—from about 100° to 120° F. (37·8—49° C.).

2. **Rest** is favourable to the coagulation of blood. Blood, of which the whole mass is kept in uniform motion, as when a closed vessel completely filled with it is constantly moved, coagulates very slowly and imperfectly.

3. **Contact with foreign matter,** and especially multiplication of the points of contact. Thus, coagulated fibrin may be quickly obtained from liquid blood by stirring it with a bundle of small twigs; and even in the living body the blood will coagulate upon rough bodies projecting into the vessels; as, for example, upon threads passed through them, or upon the heart's valves roughened by inflammatory deposits or calcareous accumulations.

4. **The free access of air.**—Coagulation is quicker in shallow than in tall and narrow vessels.

5. **The addition of less than twice the bulk of water.**

The blood last drawn is said to coagulate more quickly than the first.

The coagulation of the blood is **retarded, suspended,** or **prevented** by the following means:—

1. **Cold** retards coagulation; and so long as blood is kept at a temperature, 32° F. (0° C.), it will not coagulate at all. Freezing the blood, of course, prevents its coagulation; yet it will coagulate, though not firmly, if thawed after being frozen; and it will do so, even after it has been frozen for several months. A higher temperature than 120° F. (49° C.) retards coagulation or, by coagulating the albumen of the serum, prevents it altogether.

2. The addition of **water in greater proportion than twice the bulk** of the blood.

3. **Contact with living tissues,** and especially with the interior of a living blood-vessel.

4. **The addition of neutral salts** in the proportion of 2 or 3 per cent. and upwards. When added in large proportion most of these saline substances prevent coagulation altogether. Coagulation, however, ensues on dilution with water. The time during which blood can be thus preserved in a liquid state and coagulated by the addition of water, is quite indefinite.

5. **Imperfect aëration,**—as in the blood of those who die by asphyxia.

6. In **inflammatory states of the system** the blood coagulates more slowly although more firmly.

7. Coagulation is retarded **by exclusion of the blood from the air,** as by pouring oil on the surface, etc. In vacuo, the blood coagulates quickly; but Lister thinks that the rapidity of the process is due to the bubbling which ensues from the escape of gas, and to the blood being thus brought more freely into contact with the containing vessel.

8. The coagulation of the blood is prevented altogether **by the addition of strong acids and caustic alkalies.**

9. It has been believed, and chiefly on the authority of Hunter, **that after certain modes of death the blood does not coagulate**; he enumerates the death by lightning, over-exertion (as in animals hunted to death), blows on the stomach, fits of

anger. He says, "I have seen instances of them all." Doubtless he had done so; but the results of such events are not constant. The blood has been often observed coagulated in the bodies of animals killed by lightning or an electric shock and Gulliver has published instances in which he found clots in the hearts of hares and stags hunted to death, and of cocks killed in fighting.

Cause of the fluidity of the blood within the living body.—Very closely connected with the problem of the coagulation of the blood arises the question,—why does the blood remain liquid within the living body We have certain pathological and experimental facts, apparently opposed to one another, which bear upon it, and these may be, for the sake of clearness, classed under two heads:—

(1) *Blood will coagulate within the living body under certain conditions*,—for example, on ligaturing an artery, whereby the inner and middle coats are generally ruptured, a clot will form within it, or by passing a needle through the coats of the vessel into the blood stream a clot will gradually form upon it. Other foreign bodies, *e.g.* wire, thread, etc., produce the same effect It is a well-known fact that small clots are apt to form upon the roughened edges of the valves of the heart when the roughness has been produced by inflammation, as in endocarditis, and it is also equally true that aneurisms of arteries are sometimes spontaneously cured by the deposition within them, layer by layer, of fibrin from the blood stream, which natural cure it is the aim of the physician or surgeon to imitate.

(2) *Blood will remain liquid under certain conditions outside the body*, without the addition of any re-agent, even if exposed to the air at the ordinary temperature. It is well known that blood remains fluid in the body for some time after death, and it is only after rigor mortis has occurred that the blood is found clotted. It has been demonstrated by Hewson, and also by Lister, that if a large vein in the horse or similar animal be ligatured in two places some inches apart, and after some time be opened, the blood contained within it will be found fluid, and that coagulation will occur only after a considerable time. But this is not due to occlusion from the air simply. Lister further showed that if the vein with the blood contained within it be removed from the body, and then be carefully opened, the blood might be poured from the vein into

another similarly prepared, as from one test-tube into another, thereby suffering free exposure to the air, without coagulation occurring as long as the vessels retain their vitality. If the endothelial lining of the vein, however, be injured, the blood will not remain liquid. Again, blood will remain liquid for days in the heart of a turtle, which continues to beat for a very long time after removal from the body.

Any theory which aims at explaining the fluidity under the usual conditions of the blood within the living body must reconcile the above apparently contradictory facts, and must at the same time be made to include all the other known facts concerning the coagulation of the blood. We may therefore dismiss as insufficient the following ;—that coagulation is due to exposure to the air or oxygen ; that it is due to the cessation of the circulatory movement ; that it is due to evolution of various gases, or to the loss of heat.

Two theories, those of Lister and Brücke, remain. The former supposes that the blood has no natural tendency to clot, but that its coagulation out of the body is due to the action of foreign matter with which it happens to be brought into contact, and in the body to conditions of the tissues which cause them to act towards it like foreign matter. The latter, on the other hand, supposes that there is a natural tendency on the part of the blood to clot, but that this is restrained in the living body by some inhibitory power resident in the walls of the containing vessels.

Support was once thought to be given to Brücke's and like theories by cases of injury, in which blood extravasated in the living body has seemed to remain uncoagulated for weeks, or even months, on account of its contact with living tissues. But the supposed facts have been shown to be without foundation. The blood-like fluid in such cases is not uncoagulated blood, but a mixture of serum and blood-corpuscles, with a certain proportion of clot in various stages of disintegration. (Morrant Baker.)

As the blood must contain the substances from which fibrin is formed, and as the re-arrangement of these substances occurs very quickly whenever the blood is shed, so that it is somewhat difficult to prevent coagulation, it seems more reasonable to hold with Brücke, that the blood has a strong tendency to clot, rather than with Lister, that it has no special tendency thereto.

It has been recently suggested that the reason why blood does not coagulate in the living vessels, is that the factors which we have seen are necessary for the formation of fibrin are not in the exact state required for its production, and that the fibrin ferment is not formed or is not, at any rate, free in the living blood, but that it is produced (or set free) at the moment of coagulation by the disintegration of the colourless corpuscles. This supposition is certainly plausible, but if it be a true one, it must be assumed either that the living blood-vessels exert a restraining influence upon the disintegration of the corpuscles in sufficient numbers to form a clot, or that they render inert any small amount of fibrin ferment which may have been set free by the disintegration of a few corpuscles; as it is certain that corpuscles of all kinds must from time to time disintegrate in the blood without causing it to clot; and, secondly, that shed and defibrinated blood which contains blood corpuscles, broken down and disintegrated, will not, when injected into the vessels of an animal, produce clotting. There must be a distinct difference, therefore, if only in amount, between the normal disintegration of a few colourless corpuscles in the living uninjured blood vessels and the abnormal disintegration of a large number which occurs whenever the blood is shed without suitable precaution, or when coagulation is unrestrained by the neighbourhood of the living uninjured blood vessels.

The Blood Corpuscles or Blood-Cells.

There are two principal forms of corpuscles, the **red** and the **white**, or, as they are now frequently named, the **coloured** and the **colourless**. In the moist state, the red corpuscles form about 45 per cent. by weight, of the whole mass of the blood. The proportion of colourless corpuscles is only as 1 to 500 or 600 of the coloured.

Red or Coloured Corpuscles.—Human red blood-corpuscles are circular, biconcave disks with rounded edges, from $\frac{1}{3000}$ to $\frac{1}{4000}$ inch in diameter, and $\frac{1}{12000}$ inch in thickness, becoming flat or convex on addition of water. When viewed singly, they appear of a pale yellowish tinge; the deep red colour which they give to the blood being observable in them only when they are seen *en masse*.

They are composed of a colourless, structureless, and transparent filmy framework or *stroma*, infiltrated in all parts by a red colouring matter termed *hæmoglobin*. The *stroma* is tough and elastic, so that, as the cells circulate, they admit of elongation and other changes of form, in adaptation to the vessels, yet recover their natural shape as soon as they escape from compression. The term cell, in the sense of a bag or sac, is inapplicable to the red blood corpuscle ; and it must be considered, if not solid throughout, yet as having no such variety of consistence in different parts as to justify the notion of its being a membranous sac with fluid contents. The stroma exists in all parts of its substance, and the colouring-matter uniformly pervades this, and is not merely surrounded by and mechanically enclosed within the outer wall of the corpuscle. The red corpuscles have no nuclei, although, in their usual state, the unequal refraction of transmitted light gives the appearance of a central spot, brighter or darker than the border, according as it is viewed in or out of focus. Their specific gravity is about 1088.

Varieties.—The red corpuscles are not all alike, some being rather larger, paler, and less regular than the majority, and sometimes flat or slightly convex, with a shining particle apparent like a nucleolus. In almost every specimen of blood may be

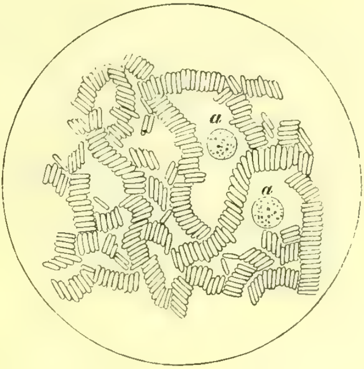

Fig. 68.—*Red corpuscles in rouleaux.* At *a*, *a*, are two white corpuscles.

also observed a certain number of corpuscles smaller than the rest. They are termed *microcytes*, and are probably immature corpuscles.

A peculiar property of the red corpuscles, exaggerated in inflammatory blood, may be here again noticed, *i.e.*, their great tendency to adhere together in rolls or columns, like piles of coins. These rolls quickly fasten together by their ends, and cluster; so that, when the blood is spread out thinly on a glass, they form a kind of irregular network, with crowds of corpuscles at the several points corresponding with the knots of the net (fig. 68). Hence, the clot formed in such a thin layer of blood looks mottled with blotches of pink upon a white ground, and in a larger quantity of such blood help, by the consequent rapid subsidence of the corpuscles, in the formation of the buffy coat already referred to.

This tendency on the part of the red corpuscles, to form rouleaux, is probably only a physical phenomenon, comparable to the collection into somewhat similar rouleaux of discs of corks when they are partially immersed in water. (Norris.)

Action of Reagents.—Considerable light has been thrown on the physical and chemical constitution of red blood-cells by studying the effects produced by mechanical means and by various reagents: the following is a brief summary of these reactions:—

Pressure.—If the red blood-cells of a frog or man are gently squeezed, they exhibit a wrinkling of the surface, which clearly indicates that there is a superficial pellicle partly differentiated from the softer mass within; again, if a needle be rapidly drawn across a drop of blood, several corpuscles will be found cut in two, but this is not accompanied by any escape of cell contents; the two halves, on the contrary, assume a rounded form, proving clearly that the corpuscles are not mere membranous sacs with fluid contents like fat-cells.

Fluids.—*Water.*—When water is added gradually to frog's blood, the oval disc-shaped corpuscles become spherical, and gradually discharge their hæmoglobin, a pale, transparent stroma being left behind; human red blood-cells change from a discoidal to a spheroidal form, and discharge their cell-contents, becoming quite transparent and all but invisible.

Saline solution (dilute) produces no appreciable effect on the

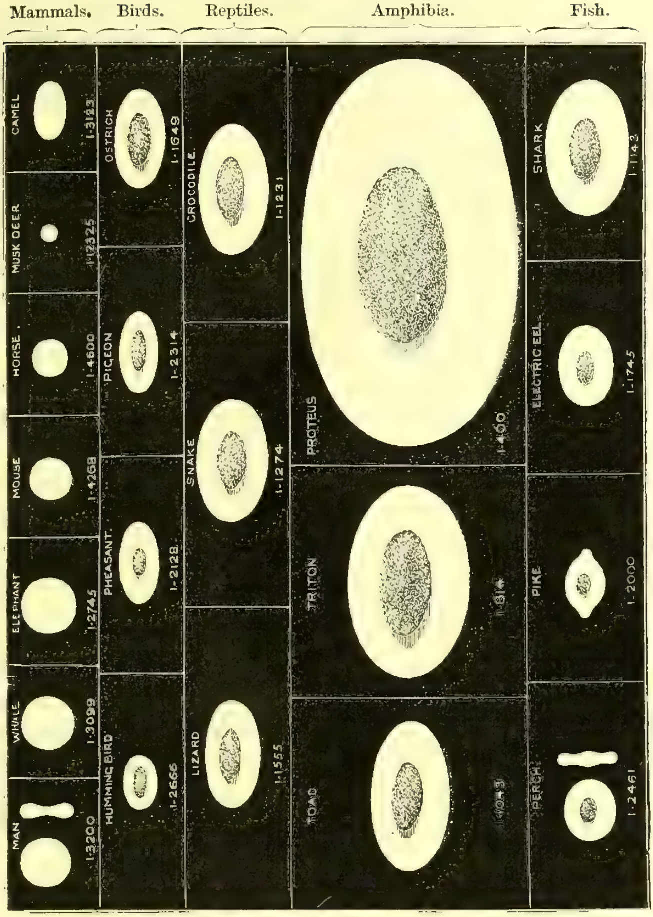

Fig. 69.*

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* The above illustration is somewhat altered from a drawing by Gulliver, in the Proceed. Zool. Society, and exhibits the typical characters of the red blood-cells in the main divisions of the Vertebrata. The fractions are those of an inch, and represent the average diameter. In the case of the oval cells, only the long diameter is here given. It is remarkable, that although the size of the red blood-cells varies so much in the different classes of the vertebrate kingdom, that of the white corpuscles remains comparatively uniform, and thus they are, in some animals, much greater, in others much less than the red corpuscles existing side by side with them.

red blood-cells of the frog. In the red blood-cells of man the discoid shape is exchanged for a spherical one, with spinous projections, like a horse-chestnut (fig. 70). Their original forms can be at once restored by the use of carbonic acid.

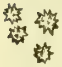
Fig. 70.

Acetic acid (dilute) causes the nucleus of the red blood cells in the frog to become more clearly defined; if the action is prolonged, the nucleus becomes strongly granulated, and all the colouring matter seems to be concentrated in it, the surrounding cell-substance and outline of the cell becoming almost invisible; after a time the cells lose their colour altogether. The cells in the figure (fig. 71) represent the successive stages of the change. A similar loss of colour occurs in the red cells of human blood, which, however, from the absence of nuclei, seem to disappear entirely.

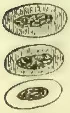
Fig. 71.

Alkalies cause the red blood-cells to swell and finally disappear.

Chloroform added to the red blood-cells of the frog causes them to part with their hæmoglobin; the stroma of the cells becomes gradually broken up. A similar effect is produced on the human red blood cell.

Tannin.—When a 2 per cent. solution of tannic acid is applied to frog's blood it causes the appearance of a sharply-defined little knob, projecting from the free surface: the colouring matter becomes at the same time concentrated in the nucleus, which grows more distinct (fig. 72). A somewhat similar effect is produced on the human red blood-cell. (Roberts.)

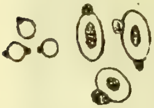
Fig. 72.

Magenta, when applied to the red blood-cells of the frog, produces a similar little knob or knobs, at the same time staining the nucleus and causing the discharge of the hæmoglobin. (Roberts.) The first effect of the magenta is to cause the discharge of the hæmoglobin, then the nucleus becomes suddenly stained, and lastly a finely granular matter issues through the wall of the corpuscle, becoming stained by the magenta, and a *macula* is formed at the point of escape. A similar macula is produced in the human red blood-cell.

Boracic acid.—A 2 per cent. solution applied to nucleated red blood-cells (frog) will cause the concentration of all the colouring matter in the nucleus; the coloured body thus formed gradually quits its central position, and comes to be partly, sometimes entirely protruded from the surface of the now colourless cell (fig. 73). The result of this experiment led Brücke to distinguish the coloured contents of the cell (zooid) from its colourless stroma (œcoid). When applied to the non-nucleated mammalian corpuscle its effect merely resembles that of other dilute acids.

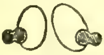
Fig. 73.

Gases—Carbonic acid.—If the red blood-cells of a frog be first exposed to the action of water-vapour (which renders their outer pellicle more readily permeable to gases), and then acted on by carbonic acid, the nuclei immediately become clearly defined and strongly granulated; when air or oxygen is admitted the original appearance is at once restored. The upper and lower cell in fig. 74 show the effect of carbonic acid; the middle one the effect of the re-admission of air. These effects can be reproduced five or six times in succession. If, however, the action of the carbonic acid be much prolonged, the granulation of the nucleus becomes permanent; it appears to depend on a coagulation of the paraglobulin. (Stricker.)

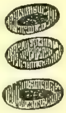
Fig. 74.

Ammonia.—Its effects seem to vary according to the degree of concentration. Sometimes the outline of the corpuscles becomes distinctly crenated; at other times the effect resembles that of boracic acid, while in other cases the edges of the corpuscles begin to break up. (Lankester.)

Heat.—The effect of heat up to 120°—140° F. (50°—60° C.) is to cause the formation of a number of bud-like processes (fig. 75).

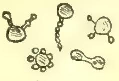
Fig. 75.

Electricity causes the red blood-corpuscles to become crenated, and at length mulberry-like. Finally they recover their round form and become quite pale.

The **general conclusions** to be drawn from these observations have been summed up as follows by Prof. Ray Lankester:—

"The red blood-corpuscle of the vertebrata is a viscid, and at the same time elastic disc, oval or round in outline, its surface being differentiated somewhat from the underlying material, and forming a pellicle or membrane of great tenuity, not distinguishable with the highest powers (whilst the corpuscle is normal and living), and having no pronounced inner limitation. The viscid mass consists of (or rather *yields*, since the state of combination of the components is not known) a variety of albuminoid and other bodies, the most easily separable of which is hæmoglobin; *secondly*, the matter which segregates to form Roberts's macula; and *thirdly*, a residuary stroma, apparently homogeneous in the mammalia (excepting as far as the outer surface or pellicle may be of a different chemical nature), but containing in the other vertebrata a sharply definable nucleus, this nucleus being already differentiated, but not sharply delineated during life, and consisting of, or separable into) at least two components, one (paraglobulin) precipitable by carbon dioxide, and removable by the action of weak ammonia; the other pellucid, and not granulated by acids."

Fig. 76.

The White or Colourless Corpuscles.—In human blood the white or colourless corpuscles or *leucocytes* are nearly spherical masses of granular protoplasm without cell wall. The granular appearance more marked in some than in others (*vide infra*), is due to the presence of particles probably of a fatty nature. In all cases one or more nuclei exist in each corpuscle. The size of the corpuscle averages $\frac{1}{2500}$ of an inch in diameter.

In health, the proportion of white to red corpuscles, which, taking an average, is about 1 to 500 or 600, varies considerably even in the course of the same day. The variations appear to depend chiefly on the amount and probably also on the kind of food taken; the number of leucocytes being very considerably increased by a meal, and diminished again on fasting. Also in young persons, during pregnancy, and after great loss of blood, there is a larger proportion of colourless blood-corpuscles, which probably shows that they are more rapidly formed under these circumstances. In old age, on the other hand, their proportion is diminished.

Varieties.—The colourless corpuscles present greater diversities of form than the red ones do. Two chief varieties are to be seen in human blood; one which contains a considerable number of granules, and the other which is paler and less granular. In size the variations are great, for in most specimens of blood it is possible to make out, in addition to he full-sized varieties, a number of smaller corpuscles, consisting of a large spherical nucleus surrounded by a variable amount of more or less granular protoplasm. The small corpuscles are, in all probability, the undeveloped forms of the others, and are derived from the cells of the lymph. Besides the above-mentioned varieties, Schmidt describes another form which he looks upon as intermediate between the coloured and the colourless forms, viz., certain corpuscles which contain red granules of hæmoglobin in their protoplasm. The different varieties of colourless corpuscles are especially well seen in the blood of frogs, newts, and other cold-blooded animals.

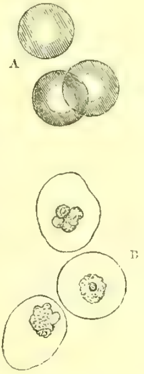

Fig. 77.—A. *Three coloured blood-corpuscles.* B. *Three colourless blood-corpuscles* acted on by acetic acid; the nuclei are very clearly visible. × 900.

Amœboid movement.—A remarkable property of the colourless corpuscles consists in their capability of spontaneously changing their shape. This was first demonstrated by Wharton Jones in the blood of the skate. If a drop of blood be examined with a high power of the microscope on a warm stage, or, in other words, under conditions by which loss of moisture is prevented, and at the same time the temperature is maintained at about that of the blood in its natural state within the walls of the living vessels, 100° F. (37·8° C.), the colourless corpuscles will be observed slowly altering their shapes, and sending out processes at various parts of their circumference. This alteration of shape, which can be most conveniently studied in the newt's blood, is called amœboid, inasmuch as it strongly resembles the movement of the lowly organized *amœba*. The processes which are sent out are either lengthened or withdrawn. If lengthened, the protoplasm of the whole corpuscle flows as it were into its process, and the corpuscle changes its position; if withdrawn, protrusion of another process at a different point of the circumference speedily follows. The change of position of the corpuscle can also take place by a flowing movement of the whole mass, and in this case the locomotion is comparatively rapid. The activity both in the processes of change of shape and also of change in position, is much more marked in some corpuscles, viz., in the granular variety than in others. Klein states that in the newt's blood the changes are especially likely to occur in a variety of the colourless corpuscle, which consists of masses of finely granular protoplasm with jagged outline, containing three or four nuclei, or of large irregular masses of protoplasm containing from five to twenty nuclei. Another phenomenon may be observed in such a specimen of blood, viz., the division of the corpuscles, which occurs in the following way. A cleft takes place in the protoplasm at one point, which becomes deeper and deeper, and then by the lengthening out and attenuation of the connection, and finally by its rupture, two corpuscles result. The nuclei have previously undergone division. The cells so formed are said to be remarkably active in their movements. Thus we see that the rounded form which the colourless corpuscles present in ordinary microscopic specimens must be looked upon as the shape natural to a dead corpuscle or to one whose vitality is dormant rather than as the shape proper to one living and active.

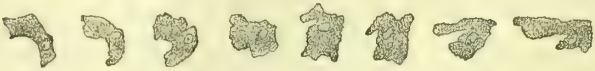

Fig. 78.—*Human colourless blood-corpuscle*, showing its successive changes of outline within ten minutes when kept moist on a warm stage. (Schofield.)

Action of re-agents upon the colourless corpuscles.—*Feeding the corpuscles.*—If some fine pigment granules, *e.g.*, powdered vermilion, be added to a fluid containing colourless blood-corpuscles, on a glass slide, these will be observed, under the microscope, to take up the pigment. In some cases colourless corpuscles have been seen with fragments of coloured ones thus embedded in their substance. This property of the colourless corpuscles is especially interesting as helping still further to connect them with the lowest forms of animal life, and to connect both with the organized cells of which the higher animals are composed.

The property which the colourless corpuscles possess of passing through the walls of the blood-vessels will be described later on.

Enumeration of the Red and White Corpuscles.—Several methods are employed for counting the blood-corpuscles, most of them depending upon the same principle, *i.e.*, the dilution of a minute volume of blood with a given volume of a colourless solution similar in specific gravity to blood serum, so that the size and shape of the corpuscles is altered as little as possible. A minute quantity of the well-mixed solution is then taken, examined under the microscope, either in a flattened capillary tube (Malassez) or in a cell (Hayem & Nachet, Gowers) of known capacity, and the number of corpuscles in a measured length of the tube, or in a given area of the cell is counted. The length of the tube and the area of the cell are ascertained by means of a micrometer scale in the microscope ocular; or in the case of Gowers' modification, by the division of the cell area into squares of known size. Having ascertained the number of corpuscles in the diluted blood, it is easy to find out the number in a given volume of normal blood. Gowers' modification of Hayem & Nachet's instrument, called by him "*Hæmacytometer*," appears to be the most convenient form of instrument for counting the corpuscles, and as such will alone be described (fig. 79). It consists of a small pipette (A), which, when filled up to a mark on its stem, holds 995 cubic millimetres. It is furnished with an india-rubber tube and glass mouth-piece to facilitate filling and emptying; a capillary tube (B) marked to hold 5 cubic millimetres, and

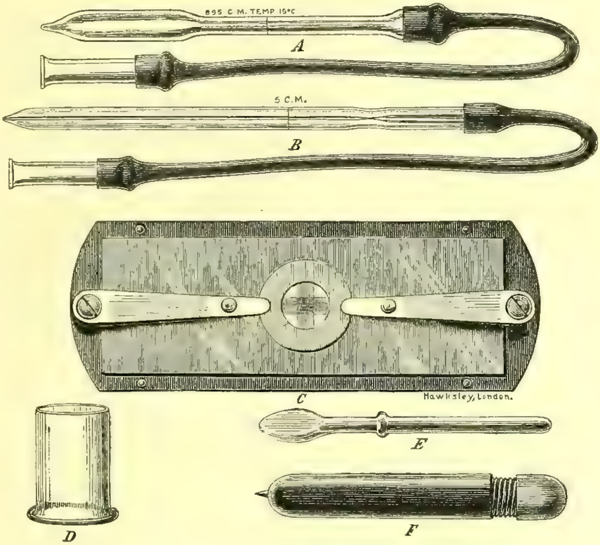

Fig. 79.—*Hæmacytometer.*

also furnished with an india-rubber tube and mouthpiece; a small glass jar (D) in which the dilution of the blood is performed; a glass stirrer (E) for mixing the blood thoroughly, (F) a needle, the length of which can be regulated by a screw; a brass stage plate (C) carrying a glass slide, on which is a cell one-fifth of a millimetre deep, and the bottom of which is divided into one-tenth millimetre squares. On the top of the cell rests the cover glass, which is kept in its place by the pressure of two springs proceeding from the stage plate. A standard saline solution of sodium sulphate, or similar salt, of specific gravity, 1025 is made, and 995 cubic millimetres are measured by means of the pipette into the glass jar, and with this five cubic millimetres of blood, obtained by pricking the finger with a needle, and measured in the capillary pipette (B), are thoroughly mixed by the glass stirring-rod. A drop of this diluted blood is then placed in the cell and covered with a cover-glass, which is fixed in position by means of the two lateral springs. The preparation is then examined under a microscope with a power of about 400 diameters, and focussed until the lines dividing the cell into squares are visible.

After a short delay, the red corpuscles which have sunk to the bottom of the cell, and are resting on the squares, are counted in ten squares, and the number of white corpuscles noted. By adding together the numbers counted in ten (one-tenth millimetre) squares the number of corpuscles in one-cubic millimetre of blood is obtained. The average number of corpuscles per each cubic millimetre of healthy blood, according to Vierordt and Welcker, is 5,000,000 in adult men, and rather fewer in women.

Chemical Composition of the Blood in Bulk.

Water		784
Solids—		
Corpuscles	130	
Proteids (of serum)	70	
Fibrin (of clot)	2·2	
Fatty matters (of serum)	1·4	
Inorganic salts (of serum)	6	
Gases, kreatin, urea and other extractive matter, glucose and accidental substances	6·4—	216
		1,000

Chemical Composition of the Red Corpuscles.—Analysis of a thousand parts of moist blood corpuscles shows the following as the result :—

Water		688
Solids—		
Organic	303·88	
Mineral	8·12—	312
		1,000

Of the solids the most important is *Hæmoglobin*, the substance to which the blood owes its colour. It constitutes, as will be seen from the appended Table, more than 90 per cent. of the organic matter of the corpuscles. Besides hæmoglobin there are proteid * and fatty matters, the former chiefly consisting of *globulins*, and the latter of *cholesterin* and *lecithin*.

In 1000 parts **organic** matter are found :—

Hæmoglobin	905·4
Proteids	86·7
Fats	7·9
	1,000·

Of the **inorganic salts of the corpuscles,** with the iron omitted—

In 1000 parts corpuscles (Schmidt) are found :—

Potassium Chloride	3·679
„ **Phosphate**	2·343
„ sulphate	·132
Sodium „	·633
Calcium „	·094
Magnesium „	·060
Soda	·341
	7·282

The properties of hæmoglobin will be considered in relation to the Gases of the blood.

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* An account of the proteid bodies, &c., will be found in the Appendix, and should be referred to for explanation of the terms employed in the text.

Chemical Composition of the Colourless Corpuscles.—In consequence of the difficulty of obtaining colourless corpuscles in sufficient number to make an analysis, little is accurately known of their chemical composition; in all probability, however, the stroma of the corpuscles is made up of proteid matter, and the nucleus of *nuclein*, a nitrogenous phosphorus-containing body akin to *mucin*, capable of resisting the action of the gastric juice. The proteid matter (globulin) is soluble in a ten per cent. solution of sodium chloride, and the solution is precipitated on the addition of water, by heat and by the mineral acids. The stroma contains *fatty granules*, and in it also the presence of *glycogen* has been demonstrated. The salts of the corpuscles are chiefly *potassium*, and of these the phosphate is in greatest amount.

Chemical Composition of the Plasma or Liquor Sanguinis.—The liquid part of the blood, the plasma or liquor sanguinis in which the corpuscles float, may be obtained in the ways mentioned under the head of the Coagulation of the Blood. In it are the fibrin factors, inasmuch as when exposed to the ordinary temperature of the air it undergoes coagulation and splits up into fibrin and serum. It differs from the serum in containing fibrinogen, but in appearance and in reaction it closely resembles that fluid; its alkalinity, however, is less than that of the serum obtained from it. It may be freed from white corpuscles by filtration at a temperature below 41° F. (5° C.).

Fibrin.—The part played by fibrin in the formation of a clot has been already described (p. 81), and it is only necessary to consider here its general properties. It is a stringy elastic substance belonging to the proteid class of bodies. It is insoluble in water and in weak saline solutions, it swells up into a transparent jelly when placed in dilute-hydrochloric acid, but does not dissolve, but in strong acid it dissolves, producing acid-albumin *; it is also soluble on boiling in strong saline solutions. Blood contains only ·2 per cent. of fibrin. It can be converted by the gastric or pancreatic juice into peptone. It possesses the power of liberating the oxygen from solutions of hydric peroxide H_2O_2. This may be shown by dipping a few shreds of fibrin in tincture of guaiacum and then immersing them in a solution of hydric peroxide. The fibrin becomes of a bluish colour, from its having liberated from the solution oxygen, which oxidises the resin of guaiacum contained in the tincture and thus produces the coloration.

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* The use of the two words **albumen** and **albumin** may need explanation. The former is the *generic* word, which may include several albuminous or proteid bodies, *e.g.*, albumen of blood; the latter which requires to be qualified by another word is the specific form, and is applied to varieties, *e.g.* egg-albumin, serum-albumin.

Salts of the Plasma.—In 1000 parts plasma there are:—

Sodium Chloride	5·546
Soda	1·532
Sodium Phosphate	·271
Potassium chloride	·359
„ sulphate	·281
Calcium phosphate	·298
Magnesium phosphate	·218
	8·505

Serum.—The serum is the liquid part of the blood or of the plasma remaining after the separation of the clot. It is an alkaline, yellowish, transparent fluid, with a specific gravity of from 1025 to 1032. In the usual mode of coagulation, part of the serum remains in the clot, and the rest, squeezed from the clot by its contraction, lies around it. Since the contraction of the clot may continue for thirty-six or more hours, the quantity of serum in the blood cannot be even roughly estimated till this period has elapsed. There is nearly as much, by weight, of serum as there is clot in coagulated blood.

Chemical Composition of the Serum.

Water . . . about	900
Proteids :	
a. Serum-albumin *β.* Paraglobulin	80
Salts. Fats—including fatty acids, cholesterin, lecithin; and some soaps Grape sugar in small amount Extractives—kreatin, kreatinin, urea, &c. Yellow pigment, which is independent of hæmoglobin Gases—small amounts of oxygen, nitrogen, and carbonic acid	20
	1000

Water.—The water of the serum varies in amount according to the amount of food, drink, and exercise, and with many other circumstances.

Proteids.—*a.* Serum-albumin is the chief proteid found in serum.

It is precipitated on heating the serum to 140° F. (60° C.), and entirely coagulates at (167° F. 75° C.), and also by the addition of strong acids, such as nitric and hydrochloric; by long contact with alcohol it is precipitated. It is not precipitated on addition of ether, and so differs from the other native albumin, viz., *egg*-albumin. When dried at 104° F. (40° C.) serum-albumin is a brittle, yellowish substance, soluble in water, possessing a lævo-rotary power of — 56°. It is with great difficulty freed from its salts, and is precipitated by solutions of metallic salts, *e.g.*, of mercuric chloride, copper sulphate, lead acetate, sodium tungstate, &c. If dried at a temperature over 167° F. (75° C.) the residue is insoluble in water, having been changed into *coagulated proteid.*

β. Paraglobulin can be obtained as a white precipitate from cold serum by adding a considerable excess of water and passing through it a current of carbonic acid gas or by the cautious addition of dilute acetic acid. It can also be obtained by saturating serum with crystallized sulphate magnesium or chloride sodium. When obtained in the latter way precipitation seems to be much more complete than by means of the former method. Paraglobulin belongs to the class of proteids called *globulins.*

The proportion of serum-albumin to paraglobulin in human blood serum is as 1·511 to 1.

The salts of sodium predominate in serum as in plasma, and of these the chloride generally forms by far the largest proportion.

Fats are present partly as fatty acids and partly emulsified. The fats are *triolein*, *tristearin*, and *tripalmitin.* The amount of fatty matter varies according to the time after, and the ingredients of, a meal. Of *cholesterin* and *lecithin* there are mere traces.

Grape sugar is found principally in the blood of the hepatic vein, about one part in a thousand.

The **extractives** vary from time to time; sometimes uric and hippuric acids are found in addition to urea, kreatin and kreatinin. Urea exists in proportion from ·02 to ·04 per cent.

The yellow *pigment* of the serum and the *odorous* matter which gives the blood of each particular animal a peculiar smell, have not yet been properly isolated.

Variations in healthy Blood under different Circumstances.

The conditions which appear most to influence the composition of the blood in health are these: Sex, Pregnancy, Age, and Temperament. The composition of the blood is also, of course, much influenced by diet.

1. *Sex.*—The blood of men differs from that of women, chiefly in being of somewhat higher specific gravity, from its containing a relatively larger quantity of red corpuscles.

2. *Pregnancy.*—The blood of pregnant women has a rather lower specific gravity than the average, from deficiency of red corpuscles. The quantity of white corpuscles, on the other hand, and of fibrin, is increased.

3. *Age.*—It appears that the blood of the fœtus is very rich in solid matter, and especially in red corpuscles; and this condition, gradually diminishing, continues for some weeks after birth. The quantity of solid matter then falls during childhood below the average, again rises during adult life, and in old age falls again.

4. *Temperament.*—But little more is known concerning the connection of this with the condition of the blood, than that there appears to be a relatively larger quantity of solid matter, and particularly of red corpuscles, in those of a plethoric or sanguineous temperament.

5. *Diet.*—Such differences in the composition of the blood as are due to the temporary presence of various matters absorbed with the food and drink, as well as the more lasting changes which must result from generous or poor diet respectively, need be here only referred to.

Effects of Bleeding.—The result of bleeding is to diminish the specific gravity of the blood; and so quickly, that in a single venesection, the portion of blood last drawn has often a less specific gravity than that of the blood that flowed first. This is, of course, due to absorption of fluid from the tissues of the body. The physiological import of this fact, namely, the instant absorption of liquid from the tissues, is the same as that of the intense thirst which is so common after either loss of blood, or the abstraction from it of watery fluid, as in cholera, diabetes, and the like.

For some little time after bleeding, the want of red corpuscles is well marked; but with this exception, no considerable alteration seems to be produced in the composition of the blood for more than a very short time: the loss of the other constituents, including the pale corpuscles, being very quickly repaired.

Variations in the Composition of the Blood, in different Parts of the Body.

The composition of the blood, as might be expected, is found to vary in different parts of the body. Thus arterial blood differs from venous ; and although its composition and general characters are uniform throughout the whole course of the systemic arteries, they are not so throughout the venous system,—the blood contained in some veins differing remarkably from that in others.

Differences between Arterial and Venous Blood.—The differences between arterial and venous blood are these :—

(*a.*) Arterial blood is bright red, from the fact that almost all its hæmoglobin is combined with oxygen (Oxyhæmoglobin, or scarlet hæmoglobin), while the purple tint of venous blood is due to the deoxidation of a certain quantity of its oxyhæmoglobin, and its consequent reduction to the purple variety (Deoxidised, or purple hæmoglobin).

(*b.*) Arterial blood coagulates somewhat more quickly.

(*c.*) Arterial blood contains more oxygen than venous, and less carbonic acid.

Some of the veins contain blood which differs from the ordinary standard considerably. These are the Portal, the Hepatic, and the Splenic veins.

Portal vein.—The blood which the portal vein conveys to the liver is supplied from two chief sources ; namely, that in the gastric and mesenteric veins, which contains the soluble elements of food absorbed from the stomach and intestines during digestion, and that in the splenic vein ; it must, therefore, combine the qualities of the blood from each of these sources.

The blood in the gastric and mesenteric veins will vary much according to the stage of digestion and the nature of the food taken, and can therefore be seldom exactly the same. Speaking generally, and without considering the sugar, dextrin, and other soluble matters which may have been absorbed from the alimentary canal, this blood appears to be deficient in solid matters especially in red corpuscles, owing to dilution by the quantity of water absorbed, to contain an excess of albumin, and to yield a less tenacious kind of fibrin than that of blood generally.

The blood from the *splenic vein* is generally deficient in red corpuscles, and contains an unusually large proportion of proteids. The fibrin obtainable from the blood seems to vary in relative amount, but to be almost always above the average. The proportion of colourless corpuscles is also unusually large. The whole quantity of solid matter is decreased, the diminution appearing to be chiefly in the proportion of red corpuscles.

The blood of the *portal vein*, combining the peculiarities of its two factors, the splenic and mesenteric venous blood, is usually of lower specific gravity than blood generally, is more watery, contains fewer red corpuscles, more proteids, and yields a less firm clot than that yielded by other blood, owing to the deficient tenacity of its fibrin.

Guarding (by ligature of the portal vein) against the possibility of an error in the analysis from regurgitation of hepatic blood into the portal vein, recent observers have determined that *hepatic venous blood* contains less water, albumen, and salts, than the blood of the portal vein; but that it yields a much larger amount of extractive matter, in which is one constant element, namely, grape-sugar, which is found, whether saccharine or farinaceous matter have been present in the food or not.

The Gases of the Blood.

The gases contained in the blood are Carbonic acid, Oxygen, and Nitrogen, 100 volumes of blood containing from 50 to 60 volumes of these gases collectively.

Arterial blood contains relatively more oxygen and less carbonic acid than venous. But the absolute quantity of carbonic acid is in both kinds of blood greater than that of the oxygen.

	Oxygen.	*Carbonic Acid.*	*Nitrogen.*
Arterial Blood . .	20 vol. per cent.	39 vol. per cent.	1 to 2 vols.
Venous " (from muscles at rest)	8 to 12 " " "	46 " " "	1 to 2 vols.

The Extraction of the Gases from the Blood.—As the ordinary air-pumps are not sufficiently powerful for the purpose, the extraction of the gases from the blood is accomplished by means of a mercurial air-pump, of which there are many varieties, those of Ludwig, Alvergnidt, Geissler, and Sprengel being the chief. The principle of action in all is much the same. Ludwig's pump, which may be taken as a type, is represented in the figure. It consists of two fixed glass globes, *C* and *F*, the upper one communicating by means of the stopcock *D*, and a stout india-rubber tube with another glass globe, *L*, which can be raised or lowered by means of a pulley; it also communicates by means of a stopcock, *B*, and a bent glass tube, *A*, with a gas receiver (not represented in the figure), *A* dipping into a bowl of mercury, so that the gas may be received over mercury. The lower globe, *F*, communicates with *C* by means of the stopcock, *E*, with *I* in which the blood is contained by the stopcock, *G*, and with a movable glass globe, *M*, similar to *L*, by means of the stopcock, *H*, and the stout india-rubber tube, *K*.

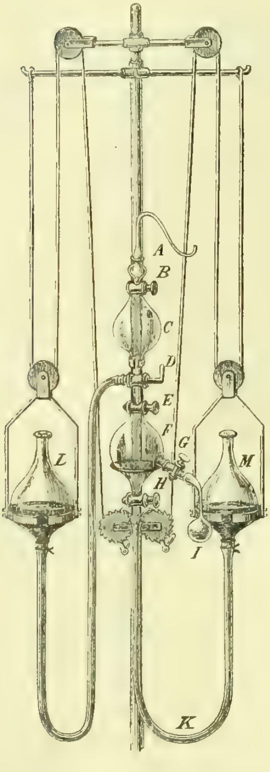

Fig. 80.—*Ludwig's Mercurial Pump.*

In order to work the pump, *L* and *M* are filled with mercury, the blood from which the gases are to be extracted is placed in the bulb *I*, the stopcocks, *H*, *E*, *D*, and *B*, being open, and *G* closed. *M* is raised by means of the pulley until *F* is full of mercury, and the air is driven out. *E* is then closed, and *L* is raised so that *C* becomes full of mercury, and the air driven off. *B* is then closed. On lowering *L* the mercury runs into it from *C*, and a vacuum is established in *C*. On opening *E* and lowering *M*, a vacuum is similarly established in *F*; if *G* be now opened, the blood in *I* will enter into ebullition, and the gases will pass off into *F* and *C*, and on raising *M* and then *L*, the stopcock *B* being opened, the gas is driven through *A*, and is received into the receiver over mercury. By repeating the experiment several times the whole of the gases of the specimen of blood is obtained, and may be estimated.

The Oxygen of the Blood.—It has been found that a very small proportion of the oxygen which can be obtained, by the aid of the mercurial pump, from the blood, exists in a state of simple solution in the plasma. If the gas were in simple solution, the amount of oxygen in any given quantity of blood exposed to any given atmosphere ought to vary with the amount of oxygen contained in the atmosphere. Since, speaking generally, the amount of any gas absorbed by a liquid such as plasma would depend upon the proportion of the gas in the atmosphere to which the liquid was exposed—if the proportion were great, the absorption would be great; if small, the absorption would be similarly small. The absorption would continue until the proportion of the gas in the liquid and in the atmosphere became equal. Other things would, of course, influence the absorption, such as the *kind of gas* employed, *nature of the liquid*, and the *temperature* of both, but *cæteris paribus*, the amount of a gas which a liquid absorbs depends upon the proportion of the gas—the so-called partial pressure—of the gas in the atmosphere to which the liquid is subjected. And conversely, if a liquid containing a gas in solution be exposed to an atmosphere containing none of the gas, the gas will be given up to the atmosphere until its amount in the liquid and in the atmosphere becomes equal. This condition is called a condition of equal tensions. The condition may be understood by a simple illustration. A large amount of carbonic acid gas is dissolved in a bottle of water by exposing the liquid to extreme pressure of the gas, and a cork is placed in the bottle and wired down. The gas exists in the water in a condition of extreme tension, and therefore there is a tendency of the gas to escape into the atmosphere, in order that the tension may be relieved; this causes the violent expulsion of the cork when the wire is removed, and if the water be placed in a glass the gas will continue to be evolved until it is almost all got rid of, and the tension of the gas in the water approximates to that of the atmosphere in which, it should be remembered, the carbon dioxide is, naturally, in very small amount, viz., ·04 per cent. Now the oxygen of the blood does not obey this law of pressure. For if blood which contains little or no oxygen be exposed to a succession of atmospheres containing more and more of that gas, we find that the absorption is at first very great, but soon becomes relatively very small, not being therefore regularly in proportion to the increased amount (or tension) of the oxygen of the atmospheres, and that conversely, if arterial blood be submitted to regularly diminishing pressures of oxygen, at first very little of the contained oxygen is given off to the atmosphere, then suddenly the gas escapes with great rapidity, again disobeying the law of pressures.

Very little oxygen can be obtained from serum freed from blood corpuscles, even by the strongest mercurial air-pump, neither can serum be made to absorb a large quantity of that gas; but the small quantity which is so given up or so absorbed follows the laws of absorption according to pressure.

It must be, therefore, evident that the chief part of the oxygen is contained in the corpuscles, and not in a state of simple solution. The chief solid constituent of the coloured corpuscles is *hæmoglobin*, which constitutes more than 90 per cent. of their bulk. This body has a very remarkable affinity for oxygen, absorbing it to a very definite extent under favourable circumstances, and giving it up when subjected to the action of reducing agents, or to a sufficiently low oxygen pressure. From these facts it is inferred that the oxygen of the blood is combined with hæmoglobin, and not simply dissolved; but inasmuch as it is comparatively easy to cause the hæmoglobin to give up its oxygen, it is believed that the oxygen is but loosely combined with the substance.

Hæmoglobin.—Hæmoglobin is a crystallizable body which constitutes by far the largest portion of the coloured corpuscles. It is intimately distributed throughout their stroma, and must be dissolved out of it before it will undergo crystallization. Its percentage composition is C. 53·85; H. 7·32; N. 16·17; O. 21·84; S. ·63; Fe. ·42; and if the molecule be supposed to contain one atom of iron the formula would be C_{600}, H_{960}, N_{154}, $Fe\ S_3\ O_{179}$. The most interesting of the properties of hæmoglobin are its powers of crystallizing and its attraction for oxygen and other gases.

Crystals.—The hæmoglobin of the blood of various animals possesses the power of crystallizing to very different extents (blood-crystals). In some animals the formation of crystals is almost spontaneous, whereas in others crystals are formed either with great difficulty or not at all. Among the animals whose blood colouring-matter crystallizes most readily are the guinea-pig, rat, squirrel, and dog; and in these cases to obtain crystals it is generally sufficient to dilute a drop of recently-drawn blood with water and expose it for a few minutes to the air. Light seems to favour the formation of the crystals. In many instances other means must be adopted, *e.g.*, the addition of alcohol, ether, or chloroform, rapid freezing, and then thawing, an electric current, a temperature of 140° F. (60° C.), or the addition of sodium sulphate.

Human blood crystallizes with difficulty, as does also that of the ox, the pig, the sheep, and the rabbit.

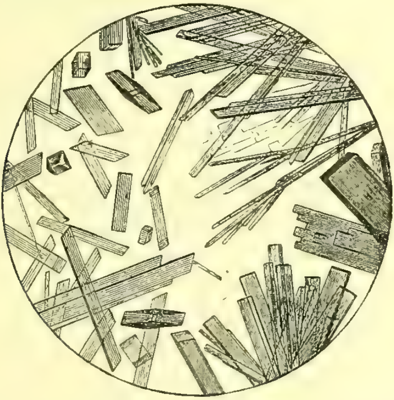

Fig. 81.—*Crystals of oxy-hæmoglobin*—prismatic from human blood.

The forms of hæmoglobin crystals, as will be seen from the appended figures, differ greatly.

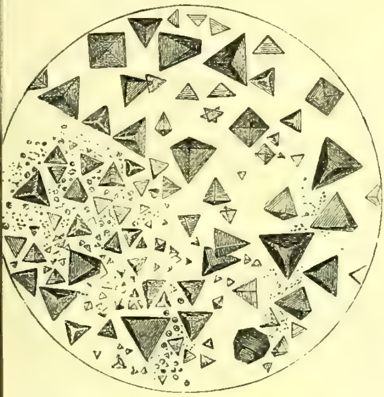

Fig. 82.—*Oxy-hæmoglobin crystals*—tetrahedral, from blood of the guinea-pig.

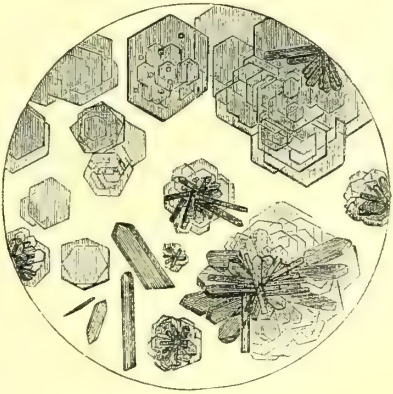

Fig. 83.—*Hexagonal oxy-hæmoglobin crystals*, from blood of squirrel. On these hexagonal plates, prismatic crystals, grouped in a stellate manner, not unfrequently occur (after Funke).

Hæmoglobin crystals are soluble in water. Both the crystals themselves and also their solutions have the characteristic colour of arterial blood.

A dilute solution of hæmoglobin gives a characteristic appearance with the spectroscope. Two absorption bands are seen between the solar lines D and E (see plate), one towards the red, with its middle line some little way to the blue side of D, is very intense, but narrower than the other, which lies near to the red side of E. Each band is darkest in the middle and fades away at the sides. As the strength of the solution increases the bands become broader and deeper, and both the red and the blue ends of the spectrum become encroached upon until the bands coalesce to form one very broad band, and only a slight amount of the green remains unabsolved, and part of the red, and on further increase of strength the former disappears.

If the crystals of oxy-hæmoglobin be subjected to a mercurial air-pump they give off a definite amount of oxygen (1 gramme giving off 1·59 c. cm. of oxygen), and they become of a purple colour; and a solution of oxy-hæmoglobin may be made to give up oxygen and to become purple in a similar manner.

This change may be also effected by passing through it hydrogen or nitrogen gas, or by the action of reducing agents, of which Stokes's fluid* is the most convenient.

With the spectroscope, a solution of deoxidized hæmoglobin is found to give an entirely different appearance from that of oxidized hæmoglobin. Instead of the two bands at D and E we find a single broader but fainter band occupying a position midway between the two, and at the same time less of the blue end of the spectrum is absorbed. Even in strong solutions this latter appearance is found, thereby differing from the strong solution of oxidised hæmoglobin which lets through only the red and orange rays; accordingly to the naked eye the one (reduced hæmoglobin solution) appears purple, the other (oxy-hæmoglobin solution) red. The deoxidised crystals or their solutions quickly absorb oxygen on exposure to the air, becoming scarlet. If solutions of blood be taken instead of solutions of hæmoglobin, results similar to the whole of the foregoing can be obtained.

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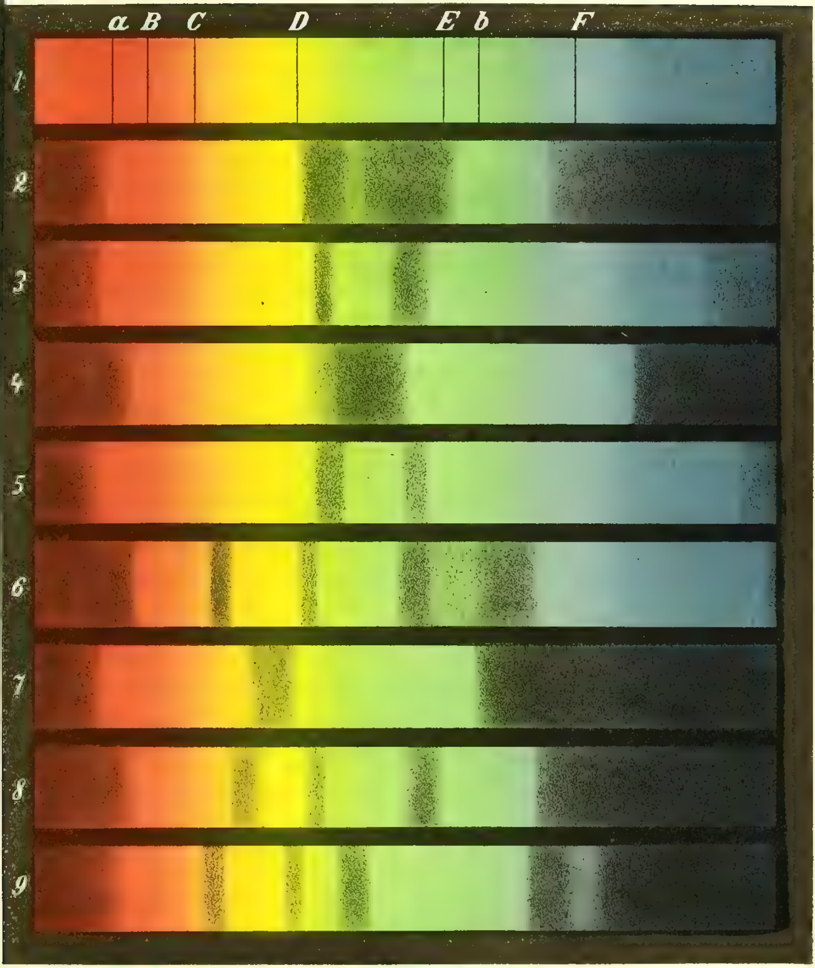
* *Stokes's Fluid* consists of a solution of *ferrous sulphate*, to which ammonia has been added and sufficient tartaric acid to prevent precipitation. Another reducing agent is a solution of *stannous chloride*, treated in a way similar to the ferrous sulphate, and a third re-agent of like nature is an aqueous solution of *ammonium sulphide*.

ABSORPTION SPECTRA



1. Spectrum of Argand lamp with Fraunhofer's lines in position.
2. Blood; i. e. a strong solution of Oxyhæmoglobin & reduced Hæmoglobin.
3. Blood more dilute.
4. Reduced Hæmoglobin. 5. Carbon Monoxide compound
6. Acid Hæmatin. 7. Alkaline Hæmatin
8. Sulphuretted Hydrogen compound. 9. Ox-bile acidulated with Acetic acid and colouring matter dissolved in Chloroform

Spectra drawn from observations by Mr W. Lepraik F.C.S.

[illegible]

Venous blood never, except in the last stages of asphyxia, fails to show the oxy-hæmoglobin bands, inasmuch as the greater part of the hæmoglobin even in venous blood exists in the more highly oxidized condition.

Action of Gases on Hæmoglobin.—*Carbonic oxide*, passed through a solution of hæmoglobin, causes it to assume a bluish colour, and the spectrum is slightly altered; two bands are still visible, but are somewhat nearer the blue end than those of oxy-hæmoglobin (see plate). The amount of carbonic oxide is equal to the amount of the oxygen displaced. Although the carbonic oxide gas readily displaces oxygen, the reverse is not the case, and upon this property depends the dangerous effect of coal gas poisoning. Coal gas contains much carbonic oxide, and this at once, when breathed, combines with the hæmoglobin of the blood, producing a compound which cannot easily be reduced, and since it is by no means an oxygen carrier, death may result from suffocation from want of oxygen notwithstanding the free entry into the lungs of pure air. Crystals of carbonic-oxide hæmoglobin closely resemble those of oxyhæmoglobin.

Nitric oxide produces a similar compound to the carbonic-oxide hæmoglobin, which is even less easily reduced.

Nitrous oxide reduces oxyhæmoglobin, and therefore leaves the reduced hæmoglobin in a condition to actively take up oxygen.

Sulphuretted Hydrogen.—If this gas be passed through a solution of oxyhæmoglobin, the hæmoglobin is reduced and an additional band appears in the red. If the solution be then shaken with air, the two bands of oxyhæmoglobin replace that of reduced hæmoglobin, but the band in the red persists.

Products of the Decomposition of Hæmoglobin.

Methæmoglobin.—If an aqueous solution of oxyhæmoglobin be exposed to the air for some time, its spectrum undergoes a change; the two D and E bands become faint, and a new line in the red at C is developed. The solution, too, has become brown and acid in reaction, and is precipitable by basic lead acetate. This change is due to the decomposition of hæmoglobin, and to the production of *methæmoglobin.* On adding ammonium sulphide, reduced hæmoglobin is produced, and on shaking this up with air, oxyhæmoglobin is reproduced.

Hæmatin.—By the action of heat, or of acids or alkalies in the presence of oxygen, hæmoglobin can be split up into a substance called *Hæmatin*, which contains all the iron of the hæmoglobin from which it was derived, and a proteid residue. Of the latter it is impossible to say more than that it is probably made up of one or more bodies of the globulin class. If there be no oxygen present, instead of hæmatin a body called *hæmochromogen* is produced, which, however, will speedily undergo oxidation into hæmatin.

Hæmatin is a dark brownish or black non-crystallizable substance of metallic lustre. Its percentage composition is C. 64·30; H. 5·50; N. 9·06; Fe, 8·82; O. 12·32; which gives the formula C_{68}, H_{70}, N_8, Fe_2, O_{10} (Hoppe-Seyler). It is insoluble in water, alcohol, and ether; soluble in the caustic alkalies; soluble with difficulty in hot alcohol to which is added sulphuric acid. The iron may be removed from hæmatin by heating it with fuming hydrochloric acid to 320° F. (160° C.), and a new body, *hæmatoporphyrin*, is produced.

In acid solution.—If to blood an excess of acetic acid be added, the colour alters to brown from decomposition of hæmoglobin, and the setting free of hæmatin; by shaking this solution with ether solution of the hæmatin is obtained. The spectrum of the etherial solution shows no less than four absorption bands, viz., one in the red between C and D, one faint and narrow close to D, and then two broader bands, one between D and E, and another nearly midway between *b* and F. The first band is by far the most distinct, and the acid solution of hæmatin without ether shows it plainly.

In alkaline solution.—The absorption band is still in the red, but nearer to D, and the blue end of the spectrum is partially absorbed to a considerable extent. If a reducing agent be added, two bands resembling those of oxyhæmoglobin, but nearer to the blue, appear; this is the spectrum of *reduced hæmatin.* On shaking the reduced hæmatin with air or oxygen the two bands are replaced by the single band of alkaline hæmatin.

Hæmatoidin.—This substance is found in the form of yellowish crystals in old blood extravasations, and is derived from the hæmoglobin. Their crystalline form and the reaction they give with nitric acid seem to show them to be identical with *Bilirubin*, the chief colouring matter of the Bile.

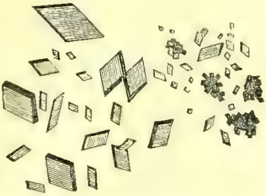


Fig. 84.—*Hæmatoidin crystals.* (Frey.)

Hæmin.—One of the most important derivatives of hæmatin is Hæmin. It is usually called *Hydrochlorate of Hæmatin* (or hydrochloride), but its exact chemical composition is uncertain. Its formula is C_{68}, H_{70}, N_8, Fe_2, O_{10}, 2 Hcl, and it contains 5·18 per cent. of chlorine, but by some it is looked upon as simply crystallized hæmatin. Although difficult to obtain in bulk, a specimen may be easily made for the microscope in the following way:—A small drop of dried blood is finely powdered with a few crystals of common salt on a glass slide, and spread out; a cover glass is then placed upon it, and glacial acetic acid added by means of a capillary pipette. The blood at once turns of a brownish colour. The slide is then heated, and the acid mixture evaporated to dryness at a high temperature. The excess of salt is washed away with water from the dried residue, and the specimen may then be mounted. A large number of small, dark, reddish black crystals of a rhombic shape, sometimes arranged in bundles, will be seen if the slide be subjected to microscopic examination.

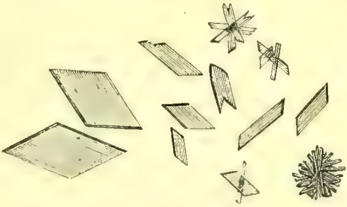


Fig. 85.—*Hæmin crystals.* (Frey.)

The formation of these hæmin crystals is of great interest and importance from a medico-legal point of view, as it constitutes the most certain and delicate test we have for the presence of blood (not of necessity the blood of man) in a stain on clothes, &c. It exceeds in delicacy even the spectroscopic test.

Estimation of Hæmoglobin.—The most exact method is by the estimation of the amount of iron in a given specimen of blood, but as this is a somewhat complicated process, a method has been proposed which, though not so exact, has the advantage of simplicity. This consists in comparing the colour of a given small amount of diluted blood with glycerine jelly tinted with carmine and picrocarmine to represent a standard solution of blood diluted one hundred times. The amount of dilution which the given blood requires will thus approximately represent the quantity of hæmoglobin it contains. (Gowers.)

Distribution of Hæmoglobin.—In connection with the ascertained function of hæmoglobin as the great oxygen-carrier, the following facts with regard to its distribution are of importance.

It occurs not only in the red blood-cells of all Vertebrata (except one fish (leptocephalus) whose blood-cells are all colourless), but also in similar cells in many Worms: moreover, it is found diffused in the vascular fluid of some other worms and certain Crustacea; it also occurs in all the striated muscles of Mammals and Birds. It is generally absent from unstriated muscle except that of the rectum. It has also been found in Mollusca in certain muscles which are specially active, viz., those which work the rasp-like tongue.

In the muscles of Fish it has hitherto only been met with in the very active muscle which moves the dorsal fin of the Hippocampus (Ray Lankester).

The Carbon Dioxide Gas in the Blood.—Of this gas in the blood, part exists in a state of simple solution in the serum, and the rest in a state of weak chemical combination. It is believed that the latter is combined with the sodium carbonate in a condition of bicarbonate. Some observers consider that part of the gas is associated with the corpuscles.

The Nitrogen in the Blood.—It is believed that the whole of the small quantity of the nitrogen contained in the blood is simply dissolved in the fluid plasma.

Development of the Blood.

The first formed blood-corpuscles of the human embryo differ much in their general characters from those which belong to the later periods of intra-uterine, and to all periods of extra-uterine life. Their manner of origin is at first very simple.

Surrounding the early embryo is a circular area, called the vascular area, in which the first rudiments of the blood-vessels and blood-corpuscles are developed. Here the nucleated embryonal cells of the mesoblast, from which the blood-vessels and corpuscles are to be formed, send out processes in various directions, and these joining together, form an irregular meshwork. The nuclei increase in number, and collect chiefly in the larger masses of protoplasm, but partly also in the processes. These nuclei gather around them a certain amount of the protoplasm, and becoming coloured, form the red blood corpuscles. The protoplasm of the cells and their branched network in which these corpuscles lie then becomes hollowed out into a system of canals enclosing fluid, in which the red nucleated corpuscles float. The corpuscles at first are from about $\frac{1}{2500}$ to $\frac{1}{1500}$ of an inch in diameter, mostly spherical, and with granular contents, and a well-marked nucleus. Their nuclei, which are about $\frac{1}{5000}$ of an

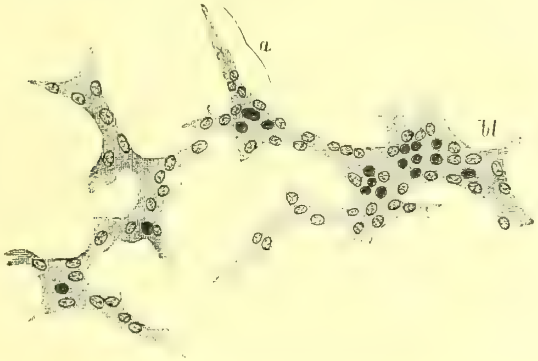


Fig. 86.—*Part of the network of developing blood-vessels in the vascular area of a guinea-pig.* *bl*, blood-corpuscles becoming free in an enlarged and hollowed out part of the network; *a*, process of protoplasm. (E. A. Schäfer.)

inch in diameter, are central, circular, very little prominent on the surfaces of the corpuscle, and apparently slightly granular or tuberculated.

The corpuscles then strongly resemble the colourless corpuscles of the fully developed blood, but are coloured. They are capable of amœboid movement and multiply by division.

When, in the progress of embryonic development, the liver begins to be formed, the multiplication of blood-cells in the whole mass of blood ceases, and new blood-cells are produced by this organ, and also by the lymphatic glands, thymus and spleen. These are at first colourless and nucleated, but afterwards acquire the ordinary blood-tinge, and resemble very much those of the first set. They also multiply by division. In whichever way produced, however, whether from the original formative cells of the embryo, or by the liver and the other organs mentioned above, these coloured nucleated cells begin very early in fœtal life to be mingled with coloured *non*-nucleated corpuscles resembling those of the adult, and at about the fourth or fifth month of embryonic existence are completely replaced by them.

Origin of the Mature Red Corpuscles.—The non-nucleated red corpuscles may possibly be derived from the nucleated, but in all probability are an entirely new formation, and the methods of

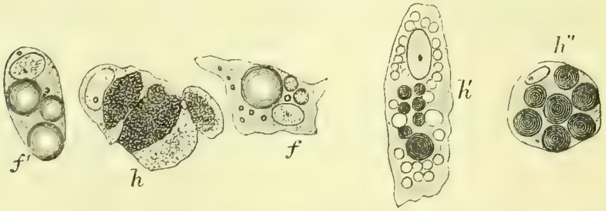


Fig. 87.—*Development of red corpuscles in connective tissue cells.* From the subcutaneous tissue of a new-born rat. h, a cell containing hæmoglobin in a diffused form in the protoplasm; h', one containing coloured globules of varying size and vacuoles; h'', a cell filled with coloured globules of nearly uniform size; f, f'', developing fat cells. (E. A. Schäfer.)

their origin are the following:—(1.) During fœtal life and possibly in some animals, *e.g.*, the rat, which are born in an immature condition, for some little time after birth, the blood discs arise in the connective tissue cells in the following way. Small globules, of varying size, of colouring matter arise in the protoplasm of the cells, and the cells themselves become branched, their branches joining the branches of similar cells. The cells next become vacuolated, and the red globules are free in a cavity filled with fluid (fig. 88); by the extension of the cavity of the cells into their processes anastomosing vessels are produced, which ultimately join with the previously existing vessels, and the globules, now having the size and appearance of the ordinary red corpuscles, are passed into the general circulation. This method of formation is called *intracellular* (Schäfer).

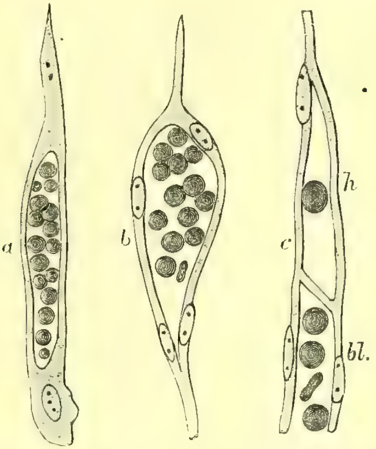


Fig. 88.—*Further development of blood-corpuscles in connective tissue cells and transformation of the latter into capillary blood-vessels.* *a*, an elongated cell with a cavity in the protoplasm occupied by fluid and by blood-corpuscles which are still globular; *b*, a hollow cell, the nucleus of which has multiplied. The new nuclei are arranged around the wall of the cavity, the corpuscles in which have now become discord; *c*, shows the mode of union of a "hæmapoietic" cell, which, in this instance, contains only one corpuscle, with the prolongation (*bl*) of a previously existing vessel; *a* and *c*, from the new-born rat; *b*, from the fœtal sheep. (E. A. Schäfer.)

(2.) *From the white corpuscles.*—The belief that the red corpuscles are derived from the white is still very general, although no new evidence has been recently advanced in favour of this view. It is, however, uncertain whether the nucleus of the white corpuscle becomes the red corpuscle, or whether the whole white corpuscle is bodily converted into the red by the gradual clearing up of its contents with a disappearance of the nucleus. Probably the latter view is the correct one.

(3.) *From the medulla of bones.*—Red corpuscles are to a very large extent derived during adult life from the large pale cells in the red marrow of bones, especially of the ribs (figs. 44, 89). These cells become coloured from the formation of hæmoglobin chiefly in one part of their protoplasm. This coloured part becomes separated from the rest of the cell and forms a red corpuscle, being at first cup-shaped, but soon taking on the normal appearance of the mature corpuscle. It is supposed that the protoplasm may grow up again and form a number of red corpuscles in a similar way.

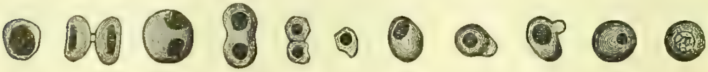


Fig. 89.—*Coloured nucleated corpuscles*, from the red marrow of the guinea-pig. (E. A. Schäfer.)

(4.) *From the tissue of the spleen.*—It is probable that red as well as white corpuscles may be produced in the spleen.

(5.) *From Microcytes.*—Hayem describes the small particles (microcytes), previously mentioned as contained in the blood (p. 94), and which he calls hæmatoblasts, as the precursors of the red corpuscles. They acquire colour, and enlarge to the normal size of red corpuscles.

Without doubt, the red corpuscles have, like all other parts of the organism, a tolerably definite term of existence, and in a like manner die and waste away when the portion of work allotted to them has been performed. Neither the length of their life, however, nor the fashion of their decay has been yet clearly made out. It is generally believed that a certain number of the red corpuscles undergo disintegration in the spleen; and indeed corpuscles in various degrees of degeneration have been observed in this organ.

Origin of the Colourless Corpuscles.—The colourless corpuscles of the blood are derived from the lymph corpuscles, being, indeed, indistinguishable from them; and these come chiefly from the lymphatic glands. Their number is increased by division.

Colourless corpuscles are also in all probability derived from the spleen and thymus, and also from the germinating endothelium of serous membranes, and from connective tissue. The corpuscles are carried into the blood either with the lymph and chyle, or pass directly from the lymphatic tissue in which they have been formed into the neighbouring blood-vessels.

Uses of the Blood.

1. To be a medium for the reception and storing of matter (ordinary food, drink, and oxygen) from the outer world, and for its conveyance to all parts of the body.
2. To be a source whence the various tissues of the body may take the materials necessary for their nutrition and maintenance; and whence the secreting organs may take the constituents of their various secretions.
3. To be a medium for the absorption of refuse matters from all the tissues, and for their conveyance to those organs whose function it is to separate them and cast them out of the body.
4. To warm and moisten all parts of the body.

Uses of the various Constituents of the Blood.

Albumen.—Albumen, which exists in so large a proportion among the chief constituents of the blood, is without doubt mainly for the nourishment of those textures which contain it or other compounds nearly allied to it.

Fibrin.—In considering the functions of fibrin, we may exclude the notion of its existence, as such, in the blood in a fluid state, and of its use in the nutrition of certain special textures, and look for the explanation of its functions to those circumstances, whether of health or disease, under which it is produced. In hæmorrhage, for example, the formation of fibrin in the clotting of blood, is the means by which, at least for a time, the bleeding is restrained or stopped; and the material or *blastema* which is produced for the permanent healing of the injured part, contains a coaguable material identical, or very nearly so, with the fibrin of clotted blood.

Fatty Matters.—The fatty matters of the blood subserve more than one purpose. For while they are the means, in part, by which the fat of the body, so widely distributed in the proper adipose and other textures, is replenished, they also, by their union with oxygen, assist in maintaining the temperature of the body. To certain secretions also, notably the milk and bile, fat is contributed.

Saline Matter.—The uses of the saline constituents of the blood are, first, to enter into the composition of such textures and secretions as naturally contain them, and, secondly, to assist in preserving the due specific gravity and alkalinity of the blood, and in preventing its decomposition. The phosphate and carbonate of sodium, to which the blood owes its alkaline reaction, increase the absorptive power of the serum for gases.

Corpuscles.—The important use of the red corpuscles is in relation to the absorption of oxygen in the lungs, and its conveyance to the tissues. How far the red corpuscles are actually concerned in the nutrition of the tissues is quite unknown.

The relation of the colourless corpuscles to the coagulation of the blood has been already considered; of their functions, other than are concerned in this phenomenon, and in the regeneration of the red corpuscles, nothing is positively known.

CHAPTER V.

THE CIRCULATION OF THE BLOOD.

THE Heart is a hollow muscular organ containing four chambers, two auricles and two ventricles, arranged in pairs. On each side (right and left) of the heart is an auricle joined to and communicating with a ventricle, but the chambers on the right side do not directly communicate with those on the left side. The circulation of the blood is chiefly carried on by the contraction of the muscular walls of these chambers of the heart, the auricles contracting simultaneously, and their contraction being followed by the simultaneous contraction of the ventricles. The blood is conveyed away from the left side of the heart by the *arteries*, and returned to the right side of the heart by the *veins*, the arteries and veins being continuous with each other at one end by means of the heart, and at the other by a fine network of vessels called the *capillaries*. The blood, therefore, in its passage from the heart passes first into the arteries, then into the capillaries, and lastly into the veins, by which it is conveyed back again to the heart, thus completing a *revolution* or *circulation*.

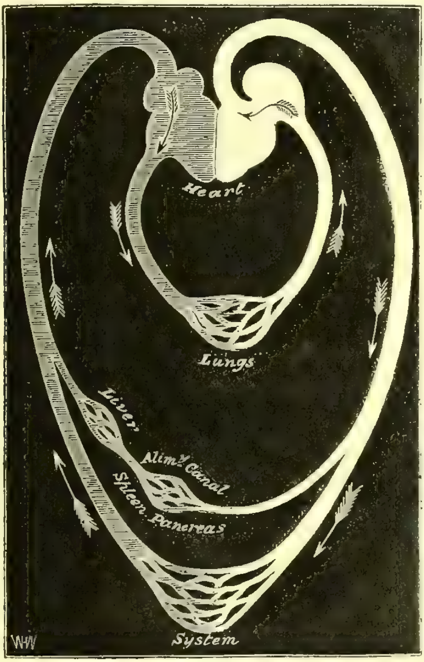


Fig. 90.—*Diagram of the Circulation.*

The right side of the heart does not directly communicate with the left to complete the entire circulation, but the blood has to pass from the right side to the lungs, through the pulmonary artery, then through the pulmonary capillary-vessels and through the pulmonary veins to the left side of the heart. Thus there are two circulations by which the blood *must* pass; the one, a shorter circuit from the right side of the heart to the lungs and back again to the left side of the heart; the other and larger circuit, from the left side of the heart to all parts of the body and back again to the right side; but more strictly speaking, there is only *one* complete circulation, which may be diagrammatically represented by a double loop, as in the accompanying figure (fig. 90).

On reference to this figure, and noticing the direction of the arrows, which represent the course of the stream of blood, it will be observed that while there is a smaller and a larger circle, both of which pass through the heart, yet that these are not distinct, one from the other, but are formed really by one continuous stream, the whole of which must, at one part of its course, pass through the lungs. Subordinate to the two principal circulations, the *Pulmonary* and *Systemic*, as they are named, it will be noticed also in the same figure that there is another, by which a portion of the stream of blood having been diverted once into the capillaries of the intestinal canal, and some other organs, and gathered up again into a single stream, is a second time divided in its passage through the liver, before it finally reaches the heart and completes a revolution. This subordinate stream through the liver is called the *Portal* circulation.

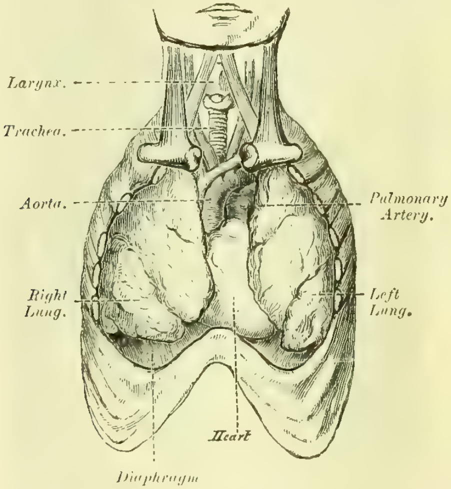


Fig. 91.—*View of heart and lungs in situ.* The front portion of the chest-wall, and the outer or *parietal* layers of the pleuræ and pericardium have been removed. The lungs are partly collapsed.

The Forces concerned in the Circulation of the Blood.—(1) The principal force provided for constantly moving the blood through the course of the circulation is that of the muscular substance of the heart; other assistant forces are (2) those of the elastic walls of the arteries, (3) the pressure of the muscles among which some of the veins run, (4) the movements of the walls of the chest in respiration, and probably, to some extent, (5) the interchange of relations between the blood and the tissues which occurs in the capillary system during the nutritive processes.

The Heart.

The Pericardium.—The heart is invested by a membranous sac—the *pericardium,* which is made up of two distinct parts, an *external* fibrous membrane, composed of closely interlacing fibres, which has its base attached to the diaphragm—both to the central tendon and to the adjoining muscular fibres, while the smaller and upper end is lost on the large blood-vessels by mingling its fibres with that of their external coats; and an *internal* serous layer, which not only lines the fibrous sac, but also is reflected on to the heart, which it completely invests. The part which lines the fibrous membrane is called the parietal layer, and that enclosing the heart, the visceral layer, and these being continuous for a short distance along the great vessels of the base of the heart, form a closed sac, the cavity of which in health contains just enough fluid to lubricate the two surfaces, and thus enable them to glide smoothly over each other during the movements of the heart. Most of the vessels passing in and out of the heart receive more or less investment from this sac.

The heart is situated in the chest behind the sternum and costal cartilages, being placed obliquely from right to left, quite two-thirds to the left of the mid-sternal line. It is of pyramidal shape, with the apex pointing downwards, outwards, and towards the left, and the base backwards, inwards, and towards the right. It rests upon the diaphragm, and its pointed apex, formed exclusively of the left side of the heart, is in contact with the chest wall, and during life beats against it at a point called the *apex beat,* situated in the fifth intercostal space, about two inches below the left nipple, and an inch and a half to the sternal side. The heart is suspended in the chest by the large vessels which proceed from its base, but, excepting the base, the organ itself lies free in the sac of the pericardium. The part which rests upon the diaphragm is flattened, and is known as the *posterior* surface, whilst the free upper part is called the *anterior* surface. The margin towards the left is thick and obtuse, whilst the lower margin towards the right is thin and acute.

On examination of the external surface the division of the heart into parts which correspond to the chambers inside of it may be traced, for a deep transverse groove called the auriculo-ventricular groove divides the auricles which form the base of the heart from the ventricles which form the remainder, including the apex, the ventricular portion being by far the greater; and, again, the inter-ventricular groove runs between the ventricles both front and back, and separates the one from the other. The anterior groove is nearer the left margin and the posterior nearer the right, as the front surface of the heart is made up chiefly of the right ventricle and the posterior surface of the left ventricle. In the furrows run the coronary vessels, which supply the tissue of the heart itself with blood, as well as nerves and lymphatics imbedded in more or less fatty tissue.

The Chambers of the Heart.—The interior of the heart is divided by a partition in such a manner as to form two chief chambers or cavities—right and left. Each of these chambers is again subdivided into an upper and a lower portion, called respectively, as already incidentally mentioned, auricle and ventricle, which freely communicate one with the other; the aperture of communication, however, being guarded by valves, so disposed as to allow blood to pass freely from the auricle into the ventricle, but not in the opposite direction. There are thus four cavities altogether in the heart—two auricles and two ventricles; the auricle and ventricle of one side being quite separate from those of the other (fig. 90).

Right Auricle.—The right auricle is situated at the right part of the base of the heart as viewed from the front. It is a thin walled cavity of more or less quadrilateral shape, prolonged at one corner into a tongue-shaped portion, the right auricular *appendix*, which slightly overlaps the exit of the great artery, the aorta, from the heart.

The interior is smooth, being lined with the general lining of the heart, the *endocardium*, and into it open the superior and inferior venæ cavæ, or great veins, which convey the blood from all parts of the body to the heart. The former is directed downwards and forwards, the latter upwards and inwards; between

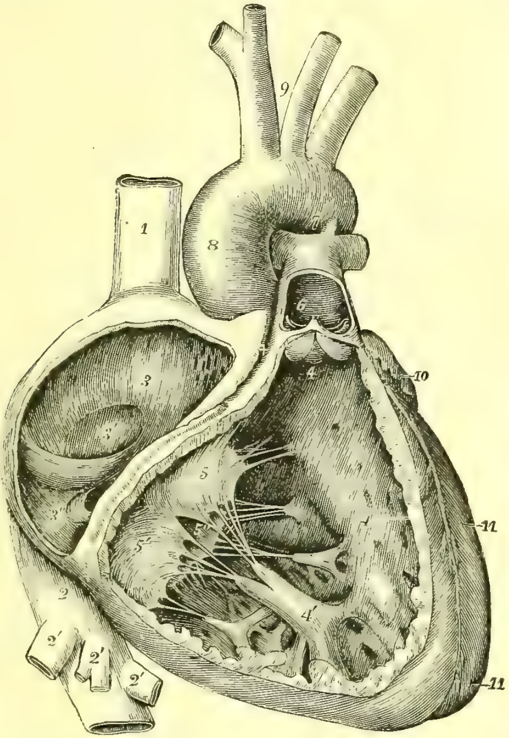


Fig. 92.—*The right auricle and ventricle opened*, and a part of their right and anterior walls removed, so as to show their interior. ½.—1, superior vena cava; 2, inferior vena cava; 2′, hepatic veins cut short; 3, right auricle; 3′, placed in the fossa ovalis, below which is the Eustachian valve; 3″, is placed close to the aperture of the coronary vein; +, +, placed in the auriculo-ventricular groove, where a narrow portion of the adjacent walls of the auricle and ventricle has been preserved; 4, 4, cavity of the right ventricle, the upper figure is immediately below the semilunar valves; 4′, large columna carnea or musculus papillaris; 5, 5′, 5″, tricuspid valve; 6, placed in the interior of the pulmonary artery, a part of the anterior wall of that vessel having been removed, and a narrow portion of it preserved at its commencement, where the semilunar valves are attached; 7, concavity of the aortic arch close to the cord of the ductus arteriosus; 8, ascending part or sinus of the arch covered at its commencement by the auricular appendix and pulmonary artery; 9, placed between the innominate and left carotid arteries; 10, appendix of the left auricle; 11, 11, the outside of the left ventricle, the lower figure near the apex (Allen Thomson).

the entrances of these vessels is a slight tubercle called *tubercle of Lower.* The opening of the inferior cava is protected and partly covered by a membrane called the *Eustachian valve.* In the posterior wall of the auricle is a slight depression called the *fossa ovalis*, which corresponds to an opening between the right and left auricles which exists in fœtal life. The right auricular appendix is of oval form, and admits three fingers. Various veins, including the coronary *sinus*, or the dilated portion of the right coronary vein, open into this chamber. In the appendix are closely set elevations of the muscular tissue covered with endocardium, and on the anterior wall of the auricle are similar elevations arranged parallel to one another, called *musculi pectinati*.

Right Ventricle.—The right ventricle occupies the chief part of the anterior surface of the heart, as well as a small part of the posterior surface: it forms the right margin of the heart. It takes no part in the formation of the apex. On section its cavity, in consequence of the encroachment upon it of the septum ventriculorum, is semilunar or crescentic (fig. 94); into it are two openings, the auriculo-ventricular at the base, and the opening of the pulmonary artery also at the base, but more to the left; the part of the ventricle leading to it is called the *conus arteriosus* or *infundibulum;* both orifices are guarded by valves, the former called *tricuspid* and the latter *semilunar* or *sigmoid*. In this ventricle are also the projections of the muscular tissue called *columnæ carneæ* (described at length p. 135).

Left Auricle.—The left auricle is situated at the left and posterior part of the base of the heart, and is best seen from behind. It is quadrilateral, and receives on either side two pulmonary veins. The auricular appendix is the only part of the auricle seen from the front, and corresponds with that on the right side, but is thicker, and the interior is more smooth. The left auricle is only slightly thicker than the right, the difference being as 1½ lines to 1 line. The left auriculo-ventricular orifice is oval, and a little smaller than that on the right side of the heart.

There is a slight vestige of the foramen between the auricles, which exists in fœtal life, on the septum between them.

Left Ventricle.—Though taking part to a comparatively slight extent in the anterior surface, the left ventricle occupies the chief part of the posterior surface. In it are two openings very close together, viz. the auriculo-ventricular and the aortic, guarded by the valves corresponding to those of the right side of the heart, viz. the *bicuspid* or *mitral* and the *semilunar* or *sigmoid*. The first

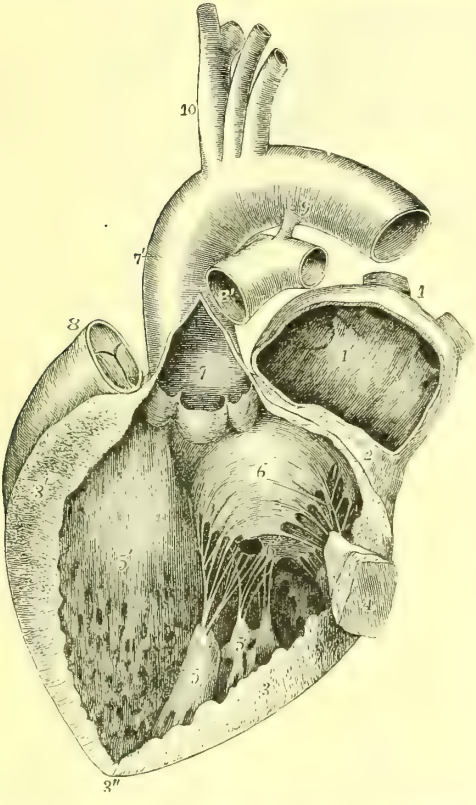


Fig. 93.—*The left auricle and ventricle opened* and a part of their anterior and left walls removed. ½.—The pulmonary artery has been divided at its commencement; the opening into the left ventricle carried a short distance into the aorta between two of the segments of the semilunar valves; and the left part of the auricle with its appendix has been removed. The right auricle is out of view. 1, the two right pulmonary veins cut short; their openings are seen within the auricle; 1', placed within the cavity of the auricle on the left side of the septum and on the part which forms the remains of the valve of the foramen ovale, of which the crescentic fold is seen towards the left hand of 1'; 2, a narrow portion of the wall of the auricle and ventricle preserved round the auriculo-ventricular orifice; 3, 3', the cut surface of the walls of the ventricle, seen to become very much thinner towards 3'', at the apex; 4, a small part of the anterior wall of the left ventricle which has been preserved with the principal anterior columna carnea or musculus papillaris attached to it; 5, 5, musculi papillares; 5', the left side of the septum, between the two ventricles, within the cavity of the left ventricle; 6, 6', the mitral valve; 7, placed in the interior of the aorta near its commencement and above the three segments of its semilunar valve which are hanging loosely together; 7', the exterior of the great aortic sinus; 8, the root of the pulmonary artery and its semilunar valves; 8', the separated portion of the pulmonary artery remaining attached to the aorta by 9, the cord of the ductus arteriosus; 10, the arteries rising from the summit of the aortic arch (Allen Thomson).

opening is at the left and back part of the base of the ventricle, and the aortic in front and towards the right. In this ventricle, as in the right, are the columnæ carneæ, which are smaller but more closely reticulated. They are chiefly found near the apex and along the posterior wall. They will be again referred to in the description of the valves. The walls of the left ventricle, which are nearly half an inch in thickness, are, with the exception of the apex, twice or three times as thick as those of the right.

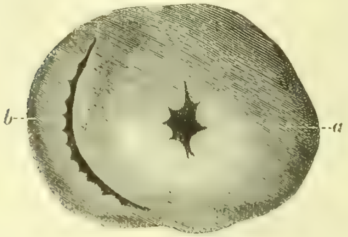


Fig. 94.—*Transverse section of bullock's heart* in a state of cadaveric rigidity. *a*, cavity of left ventricle. *b*, cavity of right ventricle. (Dalton.)

Capacity of the Chambers.—The *capacity* of the two ventricles is about four to six ounces of blood, the whole of which is impelled into their respective arteries at each contraction. The capacity of the auricles is rather less than that of the ventricles: the thickness of their walls is considerably less. The latter condition is adapted to the small amount of force which the auricles require in order to empty themselves into their adjoining ventricles; the former to the circumstance of the ventricles being partly filled with blood before the auricles contract.

Size and Weight of the Heart.—The heart is about 5 inches long, 3½ inches greatest width, and 2½ inches in its extreme thickness. The average weight of the heart in the adult is from 9 to 10 ounces; its weight gradually increasing throughout life till middle age; it diminishes in old age.

Structure.—The walls of the heart are constructed almost entirely of layers of muscular fibres; but a ring of connective tissue, to which some of the muscular fibres are attached, is inserted between each auricle and ventricle, and forms the boundary of the *auriculo-ventricular* opening. Fibrous tissue also exists at the origins of the pulmonary artery and aorta.

The muscular fibres of each auricle are in part continuous with those of the other, and partly separate; and the same remark holds true for the ventricles. The fibres of the auricles are, however, quite separate from those of the ventricles, the bond of connection between them being only the fibrous tissue of the auriculo-ventricular openings.

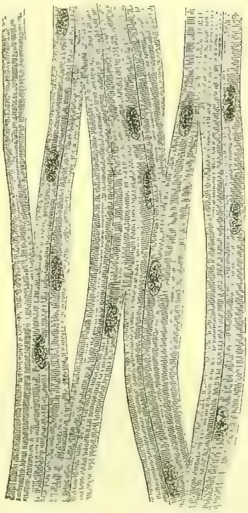


Fig. 95.—*Network of muscular fibres* (striated) from the heart of a pig. The nuclei of the muscle-corpuscles are well shown. × 450. (Klein and Noble Smith.)

The muscular fibres of the heart, unlike those of most of the involuntary muscles, are striated; but although, in this respect, they resemble the skeletal muscles, they have distinguishing characteristics of their own. The fibres which lie side by side are united at frequent intervals by short branches (fig. 95). The fibres are smaller than those of the ordinary striated muscles, and their striation is less marked. No sarcolemma can be discerned. The muscle-corpuscles are situate in the middle of the substance of the fibre; and in correspondence with these the fibres appear under certain conditions subdivided into oblong portions or "cells," the off-sets from

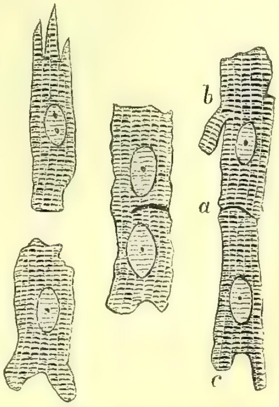


Fig. 96.—*Muscular fibre cells from the heart.* (E. A. Schäfer.)

which are the means by which the fibres anastomose one with another (fig. 96).

Endocardium.—As the heart is clothed on the outside by a thin transparent layer of pericardium, so its cavities are lined by a smooth and shining membrane, or *endocardium,* which is directly continuous with the internal lining of the arteries and veins. The endocardium is composed of connective tissue with a large admixture of elastic fibres; and on its inner surface is laid down a single tessellated layer of flattened endothelial cells. Here and there unstriped muscular fibres are sometimes found in the tissue of the endocardium.

Course of the Blood through the Heart.—The arrangement of the heart's valves is such that the blood can pass only in one direction, and this is as follows (fig. 97):—From the right auricle the blood passes into the right ventricle, and thence into the pulmonary artery, by which it is conveyed to the capillaries of the lungs. From the lungs the blood, which is now purified and altered in colour, is gathered by the pulmonary veins and taken to the left auricle. From the left auricle it passes into the left ventricle, and thence into the aorta, by which it is distributed to the capillaries

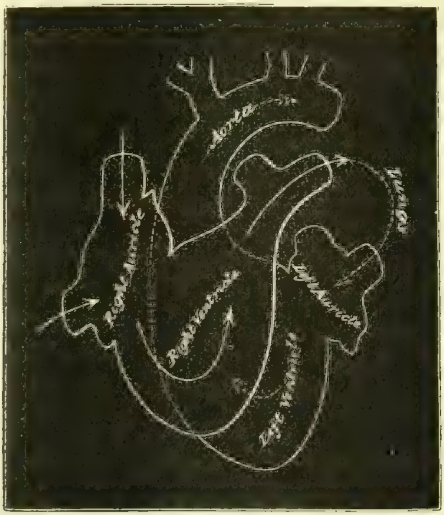


Fig. 97.—*Diagram of the circulation through the heart* (Dalton).

of every portion of the body. The branches of the aorta, from being distributed to the general system, are called *systemic* arteries; and from these the blood passes into the *systemic* capillaries, where it again becomes dark and impure, and thence into the branches of the *systemic* veins, which, forming by their union two large trunks, called the superior and inferior vena cava, discharge their contents into the right auricle, whence we supposed the blood to start.

The Valves of the Heart.—The valve between the right auricle and ventricle is named *tricuspid* (5, fig. 99), because it presents *three* principal cusps or subdivisions, and that between the left auricle and ventricle *bicuspid* (or mitral), because it has *two* such portions (6, fig. 93). But in both valves there is between each two principal portions a smaller one; so that more properly, the tricuspid may be described as consisting of six, and the mitral of four, portions. Each portion is of triangular form, its apex and sides lying free in the cavity of the ventricle, and its base, which is continuous with the bases of the neighbouring portions, so as to form an annular membrane around the auriculo-ventricular opening, being fixed to a tendinous ring which encircles the orifice between the auricle and ventricle and receives the insertions of the muscular fibres of both. In each principal cusp may be distinguished a middle-piece, extending from its base to its apex, and including about half its width, which is thicker, and much tougher and tighter than the border-pieces or edges.

While the bases of the several portions of the valves are fixed to the tendinous rings, their ventricular surfaces and borders are fastened by slender tendinous fibres, the *chordæ tendineæ*, to the walls of the ventricles, the muscular fibres of which project into the ventricular cavity in the form of bundles or columns—the *columnæ carneæ*. These columns are not all of them alike, for while some of them are attached along their whole length on one side, and by their extremities, others are attached only by their extremities; and a third set, to which the name *musculi papillares* has been given, are attached to the wall of the ventricle by one extremity only, the other projecting, papilla-like, into the cavity of the ventricle (5, fig. 93), and having attached to it *chordæ tendineæ*. Of the tendinous cords, besides those which pass from the walls of the ventricle and the musculi papillares to the margins of the valves, there are some of especial strength, which pass from the same parts to the edges of the middle and thicker portions of the cusps before referred to. The ends of these cords are spread out in the substance of the valve, giving its middle piece its peculiar strength and toughness; and from the sides numerous other more slender and branching cords are given off, which are attached all over the ventricular surface of the adjacent border-pieces of the principal portions of the valves, as well as to those smaller portions which have been mentioned as lying between each two principal ones. Moreover, the musculi papillares are so placed that, from the summit of each, tendinous cords proceed to the adjacent halves of two of the principal divisions, and to one intermediate or smaller division, of the valve.

The preceding description applies equally to the mitral and tricuspid valve; but it should be added that the mitral is considerably thicker and stronger than the tricuspid, in accordance with the greater force which it is called upon to resist.

It has been already said that while the ventricles communicate, on the one hand, with the auricles, they communicate, on the other, with the large arteries which convey the blood away from the heart; the right ventricle with the pulmonary artery (6, fig. 93), which conveys blood to the lungs, and the left ventricle with the aorta, which distributes it to the general system (7, fig. 93). And as the auriculo-ventricular orifice is guarded by valves, so are also the mouths of the pulmonary artery, and aorta (figs. 93, 99).

The semilunar valves, three in number, guard the orifice of each of these two arteries. They are nearly alike on both sides of the heart; but those of the aorta are altogether thicker and more strongly constructed than those of the pulmonary artery, in accordance with the greater pressure which they have to withstand. Each valve is of semilunar shape, its convex margin being attached to a fibrous ring at the place of junction of the artery to the ventricle, and the concave or nearly straight border being free, so that each valve forms a little pouch like a watch-pocket (7, fig. 93). In the centre of the free edge of the valve, which contains a fine cord of fibrous tissue, is a small fibrous nodule, the *corpus Arantii*, and from this and from the attached border fine fibres extend into every part of the mid substance of the valve, except a small lunated space just within the free edge, on each side of the *corpus Arantii.* Here the valve is thinnest, and composed of little more than the endocardium. Thus constructed and attached, the three semilunar valves are placed side by side around the arterial orifice of each ventricle, so as to form three little pouches, which can be separated by the blood passing out of the ventricle, but which immediately afterwards are pressed together so as to prevent any return (7, fig. 93, and 7, fig. 99). This will be again referred to. Opposite each of the semilunar cusps, both in the aorta and pulmonary artery, there is a bulging outwards of the wall of the vessel : these bulgings are called the *sinuses of Valsalva.*

Structure of the Valves.—The valves of the heart are formed essentially of thick layers of closely woven connective and elastic tissue, over which, on every part, is reflected the endocardium.

The Action of the Heart.

The heart's action in propelling the blood consists in the successive alternate contraction (systole) and relaxation (diastole) of the muscular walls of its two auricles and two ventricles.

Action of the Auricles.—The description of the action of the heart may best be commenced at that period in each action which immediately precedes the beat of the heart against the side of the chest. For at this time the whole heart is in a passive state, the walls of both auricles and ventricles are relaxed, and their cavities are being dilated. The auricles are gradually filling with blood flowing into them from the veins ; and a portion of this blood passes at once through them into the ventricles, the opening between the cavity of each auricle and that of its corresponding ventricle being, during all the *pause*, free and patent. The auricles, however, receiving more blood than at once passes through them to the ventricles, become, near the end of the pause, fully distended ; and at the end of the pause, they contract and expel their contents into the ventricles.

The contraction of the auricles is sudden and very quick ; it commences at the entrance of the great veins into them, and is thence propagated towards the auriculo-ventricular opening ; but the last part which contracts is the auricular appendix. The effect of this contraction of the auricles is to quicken the flow of blood from them into the ventricles; the force of their contraction not being sufficient under ordinary circumstances to cause any back-flow into the veins. The reflux of blood into the great veins is, moreover, resisted not only by the mass of blood in the veins and the force with which it streams into the auricles, but also by the simultaneous contraction of the muscular coats with which the large veins are provided near their entrance into the auricles. Any slight regurgitation from the right auricle is limited also by the valves at the junction of the subclavian and internal jugular veins, beyond which the blood cannot move backwards; and the coronary vein is preserved from it by a valve at its mouth.

In birds and reptiles regurgitation from the right auricle is prevented by valves placed at the entrance of the great veins.

During the auricular contraction the force of the blood propelled into the ventricle is transmitted in all directions, but being insufficient to separate the semilunar valves, it is expended in distending the ventricle, and, by a reflux of the current, in raising and gradually closing the auriculo-ventricular valves, which, when the ventricle is full, form a complete septum between it and the auricle.

Action of the Ventricles.—The blood which is thus driven, by the contraction of the auricles, into the corresponding ventricles, being added to that which had already flowed into them during the heart's pause, is sufficient to complete their diastole. Thus distended, they immediately contract: so immediately, indeed, that their systole looks as if it were continuous with that of the auricles. The ventricles contract much more slowly than the auricles, and in their contraction probably always thoroughly empty themselves, differing in this respect from the auricles, in which, even after their complete contraction, a small quantity of blood remains. The shape of both ventricles during systole undergoes an alteration, the left probably not altering in length but to a certain degree in breadth, the diameters in the plane of the base being diminished. The right ventricle does actually shorten to a small extent. The systole has the effect of diminishing the diameter of the base, especially in the plane of the auriculo-ventricular valves; but the length of the heart as a whole is not altered. (Ludwig.) During the systole of the ventricles, too, the aorta and pulmonary artery, being filled with blood by the force of the ventricular action against considerable resistance, elongate as well as expand, and the whole heart moves slightly towards the right and forwards, twisting on its long axis, and exposing more of the left ventricle anteriorly than is usually in front. When the systole ends the heart resumes its former position, rotating to the left again as the aorta and pulmonary artery contract.

Functions of the Auriculo-Ventricular Valves.—The distension of the ventricles with blood continues throughout the whole period of their diastole. The auriculo-ventricular valves are gradually brought into place by some of the blood getting behind the cusps and floating them up ; and by the time that the diastole is complete, the valves are no doubt in apposition, the completion of this being brought about by the reflex current caused by the systole of the auricles. This elevation of the auriculo-ventricular valves is, no doubt, materially aided by the action of the elastic tissue which has been shown to exist so largely in their structure, especially on the auricular surface. At any rate at the *commencement* of the ventricular systole they are completely closed. It should be recollected that the diminution in the breadth of the base of the heart in its transverse diameters during ventricular systole is especially marked in the neighbourhood of the auriculo-ventricular rings, and thus aids in rendering the auriculo-ventricular valves competent to close the openings, by greatly diminishing their diameter. The margins of the cusps of the valves are still more secured in apposition with another, by the simultaneous contraction of the musculi papillares, whose chordæ tendineæ have a special mode of attachment for this object (p. 136). As in the case of the semilunar valves to be immediately described, the auriculo-ventricular valves meet not by their *edges* only, but by the opposed surfaces of their thin outer borders. The semilunar valves, on the other hand, which are closed in the intervals of the ventricle's contraction (fig. 92, 6), are forced apart by the same pressure that tightens the auriculo-ventricular valves; and, thus, the whole force of the contracting ventricles is directed to the expulsion of blood through the aorta and pulmonary artery.

The form and position of the fleshy columns on the internal walls of the ventricle no doubt help to produce this obliteration of the cavity during their contraction; and the completeness of the closure may often be observed on making a transverse section of a heart shortly after death, in any case in which the contraction of the *rigor mortis* is very marked (fig. 94). In such a case only a central fissure may be discernible to the eye in the place of the cavity of each ventricle.

If there were only circular fibres forming the ventricular wall, it is evident that on systole the ventricle would elongate; if there were only longitudinal fibres the ventricle would shorten on systole; but there are both. The tendency to alter in length is thus counter-balanced, and the whole force of the contraction is expended in diminishing the cavity of the ventricle; or, in other words, in expelling its contents.

On the conclusion of the systole the ventricular walls tend to expand by virtue of their elasticity, and a negative pressure is set up, which tends to suck in the blood. This negative or suctional pressure on the left side of the heart is of the highest importance in helping the pulmonary circulation. It has been found to be equal to 23 mm. of mercury, and is quite independent of the aspiration or suction power of the thorax in aiding the blood-flow to the heart, to be described in the chapter on Respiration.

Function of the Musculi Papillares.—The special function of the *musculi papillares* is to prevent the auriculo-ventricular valves from being everted into the auricle. For the chordæ tendineæ might allow the valves to be pressed back into the auricle, were it not that when the wall of the ventricle is brought by its contraction nearer the auriculo-ventricular orifice, the musculi papillares more than compensate for this by their own contraction—holding the cords tight, and, by pulling down the valves, adding slightly to the force with which the blood is expelled.

What has been said applies equally to the auriculo-ventricular valves on both sides of the heart, and of both alike the closure is generally complete every time the ventricles contract. But in some circumstances the closure of the tricuspid valve is not complete, and a certain quantity of blood is forced back into the auricle. This has been called the *safety-valve action* of this valve. The circumstances in which it usually happens are those in which the vessels of the lung are already full enough when the right ventricle contracts, as *e.g.*, in certain pulmonary diseases, in very active exertion, and in great efforts. In these cases, the tricuspid valve does not completely close, and the regurgitation of the blood may be indicated by a pulsation in the jugular veins synchronous with that in the carotid arteries.

Function of the Semilunar Valves.—The arterial or semilunar valves are forced apart by the out-streaming blood, with which the contracting ventricle dilates the large arteries. The dilation of the arteries is, in a peculiar manner, adapted to bring the valves into action. The lower borders of the semilunar valves are attached to the inner surface of a tendinous ring, which is, as it were, inlaid at the orifice of the artery, between the muscular fibres of the ventricle and the elastic fibres of the walls of the artery. The tissue of this ring is tough, and does not admit of extension under such pressure as it is commonly exposed to; the valves are equally inextensile, being, as already mentioned, formed of tough, close-textured, fibrous tissue, with strong interwoven cords, and covered with *endocardium.* Hence, when the ventricle propels blood through the orifice and into the canal of the artery, the lateral pressure which it exercises is sufficient to dilate the walls of the artery, but not enough to stretch in an equal degree, if at all, the unyielding valves and the ring to which their lower borders are attached. The effect, therefore, of each such propulsion of blood from the ventricle is, that the wall of the first portion of the artery is dilated into three pouches behind the valves, while the free margins of the valves are drawn inward towards its centre (fig. 98, B). Their positions may be explained by the diagrams, in which the continuous lines represent a transverse section of the arterial walls, the dotted ones the edges of the valves, firstly, when the valves are nearest to the walls (A), and, secondly, when, the walls being dilated, the valves are drawn away from them (B).

This position of the valves and arterial walls is retained so long as the ventricle continues in contraction: but, as soon as it relaxes, and the dilated arterial walls can recoil by their elasticity, the blood is forced backwards towards the ventricles as onwards in the course of the circulation. Part of the blood thus forced back lies in the pouches (sinuses of Valsalva) (*a*, fig. 98, B) between the valves and the arterial walls; and the valves are by it pressed together till their thin lunated margins meet in three lines radiating from the centre to the circumference of the artery (7 and 8, fig. 99).

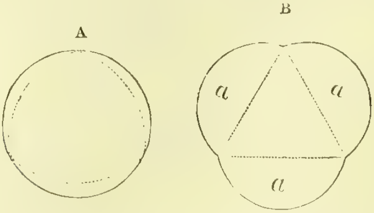


Fig. 98.—*Sections of aorta*, to show the action of the semilunar valves. A is intended to show the valves, represented by the dotted lines, pressed towards the arterial walls, represented by the continuous outer line. B (after Hunter) shows the arterial wall distended into three pouches (*a*), and drawn away from the valves, which are straightened into the form of an equilateral triangle, as represented by the dotted lines.

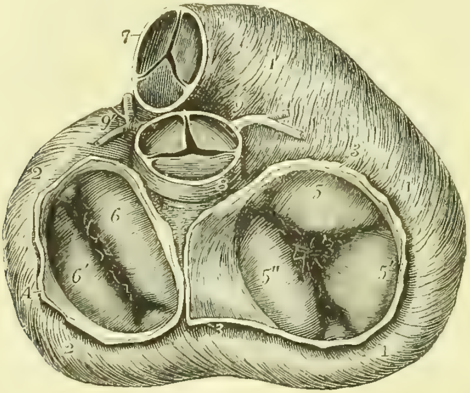


Fig. 99.—*View of the base of the ventricular part of the heart*, showing the relative position of the arterial and auriculo-ventricular orifices.—⅔. The muscular fibres of the ventricles are exposed by the removal of the pericardium, fat, blood-vessels, etc.; the pulmonary artery and aorta have been removed by a section made immediately beyond the attachment of the semilunar valves, and the auricles have been removed immediately above the auriculo-ventricular orifices. The semilunar and auriculo-ventricular valves are in the nearly closed condition. 1, 1, the base of the right ventricle; 1′, the conus arteriosus; 2, 2, the base of the left ventricle; 3, 3, the divided wall of the right auricle; 4, that of the left; 5, 5′, 5″, the tricuspid valve; 6, 6′, the mitral valve. In the angles between these segments are seen the smaller fringes frequently observed; 7, the anterior part of the pulmonary artery; 8, placed upon the posterior part of the root of the aorta; 9, the right, 9′, the left coronary artery. (Allen Thomson.)

The contact of the valves in this position, and the complete closure of the arterial orifice, are secured by the peculiar construction of their borders before mentioned. Among the cords which are interwoven in the substance of the valves, are two of greater strength and prominence than the rest; of which one extends along the free border of each valve, and the other forms a double curve or festoon just below the free border. Each of these cords is attached by its outer extremities to the outer end of the free margin of its valve, and in the middle to the corpus Arantii; they thus enclose a lunated space from a line to a line and a half in width, in which space the substance of the valve is much thinner and more pliant than elsewhere. When the valves are pressed down, all these parts or spaces of their surfaces come into contact, and the closure of the arterial orifice is thus secured by the apposition not of the mere edges of the valves, but of all those thin lunated parts of each which lie between the free edges and the cords next below them These parts are firmly pressed together, and the greater the pressure that falls on them the closer and more secure is their apposition. The corpora Arantii meet at the centre of the arterial orifice when the valves are down, and they probably assist in the closure; but they are not essential to it, for, not unfrequently, they are wanting in the valves of the pulmonary artery, which are then extended in larger, thin, flapping margins. In valves of this form, also, the inlaid cords are less distinct than in those with corpora Arantii; yet the closure by contact of their surfaces is not less secure.

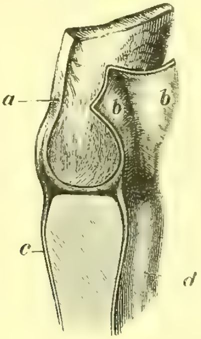


Fig. 100.—*Vertical section through the aorta* at its junction with the left ventricle. *a*, Section of aorta. *bb*, Section of two valves. *c*, Section of wall of ventricle. *d*, Internal surface of ventricle.

It has been clearly shown that this pressure of the blood is not entirely sustained by the valves alone, but in part by the muscular substance of the ventricle (Savory). By making vertical sections (fig. 100) through various parts of the tendinous rings it is possible to show clearly that the aorta and pulmonary artery, expanding towards their termination, are situated upon the *outer* edge of the thick upper border of the ventricles, and that consequently the portion of each semilunar valve adjacent to the vessel passes over and rests upon the muscular substance—being thus supported, as it were, on a kind of muscular floor formed by the upper border of the ventricle. The result of this arrangement is that the reflux of the blood is most efficiently sustained by the ventricular wall.*

As soon as the auricles have completed their contraction they begin again to dilate, and to be refilled with blood, which flows into them in a steady stream through the great venous trunks. They are thus filling during all the time in which the ventricles are contracting; and the contraction of the ventricles being ended, these also again dilate, and receive again the blood that flows into them from the auricles. By the time that the ventricles are thus from one-third to two-thirds full, the auricles are distended; these, then suddenly contracting, fill up the ventricles, as already described (p. 137).

Cardiac Revolution.—If we suppose a cardiac revolution divided into five parts, *one* of these will be occupied by the contraction of the auricles, *two* by that of the ventricles, and two by repose of both auricles and ventricles.

Contraction of Auricles . . .	1 +	Repose of Auricles . . .	4 = 5
„ Ventricles . .	2 +	„ Ventricles . .	3 = 5
Repose (no contraction of either auricles or ventricles) . . .	2 +	Contraction (of either auricles or ventricles) . .	3 = 5
	— 5		

If the speed of the heart be quickened, the time occupied by each cardiac revolution is of course diminished, but the diminution affects only the diastole and pause. The systole of the ventricles occupies very much the same time, about $\frac{4}{10}$ sec., whatever the pulse-rate.

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* Savory's preparations, illustrating this and other points in relation to the structure and functions of the valves of the heart, are in the Museum of St. Bartholomew's Hospital.

The periods in which the several valves of the heart are in action may be connected with the foregoing table; for the auriculo-ventricular valves are closed, and the arterial valves are open during the whole time of the ventricular contraction, while, during the dilation and distension of the ventricles the latter valves are shut, the former open. Thus whenever the auriculo-ventricular valves are open, the arterial valves are closed and *vice versâ.*

Sounds of the Heart.

When the ear is placed over the region of the heart, two *sounds* may be heard at every beat of the heart, which follow in quick succession, and are succeeded by a *pause* or period of silence. The *first* sound is dull and prolonged; its commencement coincides with the impulse of the heart, and just precedes the pulse at the wrist. The *second* is a shorter and sharper sound, with a somewhat flapping character, and follows close after the arterial pulse. The period of time occupied respectively by the two sounds taken together, and by the pause, are almost exactly equal. The relative length of time occupied by each sound, as compared with the other, is a little uncertain. The difference may be best appreciated by considering the different forces concerned in the production of the two sounds. In one case there is a strong, comparatively slow, contraction of a large mass of muscular fibres, urging forward a certain quantity of fluid against considerable resistance; while in the other it is a strong but shorter and sharper recoil of the elastic coat of the large arteries,—shorter because there is no resistance to the flapping back of the semilunar valves, as there was to their opening. The sounds may be expressed by saying the words *lŭbb—dŭp* (C. J. B. Williams).

The events which correspond, in point of time, with the *first* sound, are (1) the contraction of the ventricles, (2) the first part of the dilatation of the auricles, (3) the closure of the auriculo-ventricular valves, (4) the opening of the semilunar valves, and (5) the propulsion of blood into the arteries. The sound is succeeded, in about one-thirtieth of a second, by the pulsation of the facial arteries, and in about one-sixth of a second, by the pulsation of the arteries at the wrist. The *second* sound, in point of time, immediately follows the cessation of the ventricular contraction, and corresponds with (*a*) the closure of the semilunar valves, (*b*) the continued dilatation of the auricles, (*c*) the commencing dilatation of the ventricles, and (*d*) the opening of the auriculo-ventricular valves. The *pause* immediately follows the second sound, and corresponds *in its first part* with the completed distension of the auricles, and *in its second* with their contraction, and the completed distension of the ventricles ; the auriculo-ventricular valves being, all the time of the pause, open, and the arterial valves closed.

Causes.—The chief cause of the first sound of the heart appears to be the vibration of the auriculo-ventricular valves, due to their stretching, and also, but to a less extent, of the ventricular walls, and coats of the aorta and pulmonary artery, all of which parts are suddenly put into a state of tension at the moment of ventricular contraction. The effect may be intensified by the *muscular sound* produced by contraction of the mass of muscular fibres which form the ventricle.

The cause of the *second* sound is more simple than that of the first. It is probably due entirely to the sudden closure and *consequent vibration* of the semilunar valves when they are pressed down across the orifices of the aorta and pulmonary artery. The influence of the valves in producing the sound is illustrated by the experiment performed on large animals, such as calves, in which the results could be fully appreciated. In these experiments two delicate curved needles were inserted, one into the aorta, and another into the pulmonary artery, below the line of attachment of the semilunar valves, and, after being carried upwards about half an inch, were brought out again through the coats of the respective vessels, so that in each vessel one valve was included between the arterial walls and the wire. Upon applying the stethoscope to the vessels, after such an operation, the second sound had ceased to be audible. Disease of these valves, when so extensive as to interfere with their efficient action, also often demonstrates the same fact by modifying or destroying the distinctness of the second sound.

One reason for the second sound being a clearer and sharper one than the first may be, that the semilunar valves are not covered in by the thick layer of fibres composing the walls of the heart to such an extent as are the *auriculo-ventricular*. It might be expected therefore that their vibration would be more easily heard through a stethoscope applied to the walls of the chest.

The contraction of the auricles which takes place in the end of the pause is inaudible outside the chest, but may be heard, when the heart is exposed and the stethoscope placed on it, as a slight sound preceding and continued into the louder sound of the ventricular contraction.

The Impulse of the Heart.—At the commencement of each ventricular contraction, the heart may be felt to beat with a slight shock or *impulse* against the walls of the chest. The force of the impulse, and the extent to which it may be perceived beyond this point, vary considerably in different individuals, and in the same individual under different circumstances. It is felt more distinctly, and over a larger extent of surface, in emaciated than in fat and robust persons, and more during a forced expiration than in a deep inspiration; for, in the one case, the intervention of a thick layer of fat or muscle between the heart and the surface of the chest, and in the other the inflation of the portion of lung which overlaps the heart, prevents the impulse from being fully transmitted to the surface. An excited action of the heart, and especially a hypertrophied condition of the ventricles, will increase the impulse; while a depressed condition, or an atrophied state of the ventricular walls, will diminish it.

Cause of the Impulse.—During the period which precedes the ventricular systole, the apex of the heart is situated upon the diaphragm and against the chest-wall in the fifth intercostal space. When the ventricles contract, their walls become hard and tense, since to expel their contents into the arteries is a distinctly laborious action, as it is resisted by the tension within the vessels. It is to this sudden hardening that the impulse of the heart against the chest-wall is due, and the shock of the sudden tension may be felt not only externally, but also internally, if the abdomen of an animal be opened and the finger be placed upon the under surface of the diaphragm, at a point corresponding to the under surface of the ventricle. The shock is felt, and possibly seen more distinctly because of the partial rotation of the heart, already spoken of, along its long axis towards the right. The movement produced by the ventricular contraction may be registered by means of an instrument called the *cardiograph*, and it will be found to correspond almost exactly with a tracing obtained by the same instrument applied over the contracting ventricle itself.

The *Cardiograph* (fig. 101) consists of a cup-shaped metal box over the open front of which is stretched an elastic membrane upon which is fixed a small knob of hard wood or ivory. This knob, however, may be attached instead, as in the figure, to the side of the box by means of a spring, and may be made to act upon a metal disc attached to the elastic membrane.

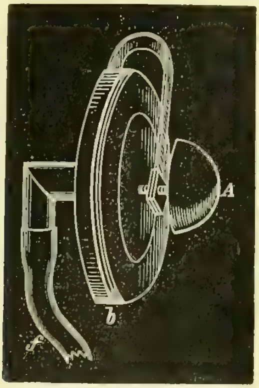

Fig. 101.—*Cardiograph.* (Sanderson's.)

The knob (A) is for application to the chest-wall over the place of the greatest impulse of the heart. The box or *tympanum* communicates by means of an air-tight elastic tube (f) with the interior of a second tympanum (fig. 102, b), in connection with which is a long and light lever (a). The shock of the heart's impulse being communicated to the ivory knob, and through it to the first tympanum, the effect is, of course, at once transmitted by the column of air in the elastic tube to the interior of the second tympanum, also closed, and through the elastic and movable lid of the latter to the lever, which is placed in connection with a registering apparatus, which consists generally of a cylinder or drum covered with smoked paper, revolving according to a definite velocity by clock-work. The point of the lever writes upon the paper, and a tracing of the heart's impulse is thus obtained.

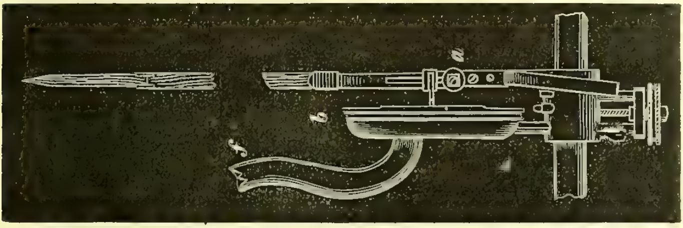

Fig. 102.—*Marey's Tambour* (*b*), to which the movement of the column of air in the first tympanum is conducted by the tube, *f*, and from which it is communicated by the lever, *a*, to a revolving cylinder, so that the tracing of the movement of the impulse beat is obtained.

By placing three small india-rubber air-bags in the interior respectively of the right auricle, the right ventricle, and in an intercostal space in front of the heart of living animals (horse), and placing these bags, by means of long narrow tubes, in communication with three levers, arranged one over the other in connection with a registering apparatus (fig. 104), MM. Chauveau and Marey have been able to measure with much accuracy the variations of the endocardial pressure and the comparative duration of the contractions of the auricles and ventricles. By means of the same apparatus, the synchronism of the impulse with the contraction of the ventricles, is also well shown ; and the causes of the several vibrations of which it is really composed, have been discovered.

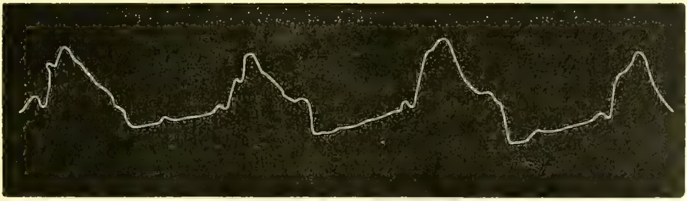

Fig. 103.—*Tracing of the impulse of the heart of man.* (Marey.)

In the tracing (fig 105), the intervals between the vertical lines represent periods of a tenth of a second. The parts on which any given vertical line falls represent, of course, simultaneous events. Thus,—it will be seen that the contraction of the auricle, indicated by the upheaval of the tracing at A in first tracing, causes a slight increase of pressure in the ventricle (A′ in second tracing), and produces a tiny impulse (A″ in third tracing). So also, the closure of the semilunar valves, while it causes a momentarily increased pressure in the ventricle at D′, does not fail to affect

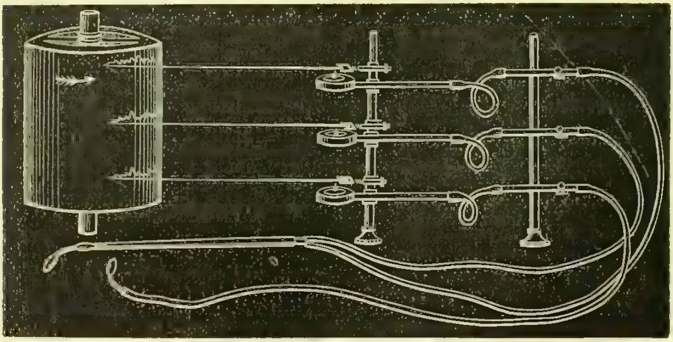

Fig. 104.—*Apparatus of MM. Chauveau and Marey* for estimating the variations of endocardial pressure, and production of impulse of the heart.

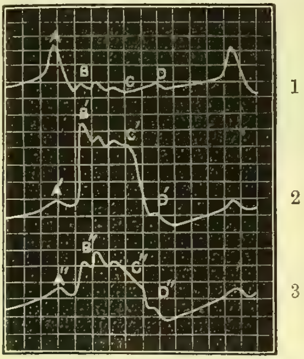

Fig. 105.—*Tracings of* (1), *Intra-auricular, and* (2), *Intra-ventricular pressures, and* (3), *of the impulse of the heart*, to be read from left to right, obtained by Chauveau and Marey's apparatus.

the pressure in the auricle D, and to leave its mark in the tracing of the impulse also, D″.

The large upheaval of the ventricular and the impulse tracings, between A′ and D′, and A″ and D″, are caused by the ventricular contraction, while the smaller undulations, between B and C, B′ and C′, B″ and C″, are caused by the vibrations consequent on the tightening and closure of the auriculo-ventricular valves.

Although, no doubt, the method thus described may show a perfectly correct view of the endo-cardiac pressure variations, it should be recollected that the muscular walls may grip the air-bags, even after the complete expulsion of the contents of the chamber, and so the lever might remain for a too long time in the position of extreme tension, and would represent on the tracing not only, as it ought to do, the auricular or ventricular pressure on the blood, but, also afterwards, the muscular pressure exerted upon the bags themselves. (M. Foster.)

Frequency and Force of the Heart's Action.

The heart of a healthy adult man contracts from seventy to seventy-five times in a minute; but many circumstances cause this rate, which of course corresponds with that of the arteria *pulse*, to vary even in health. The chief are age, temperament, sex, food and drink, exercise, time of day, posture, atmospheric pressure, temperature.

Age.—The frequency of the heart's action gradually diminishes from the commencement to near the end of life, but is said to rise again somewhat in extreme old age, thus :—

Before birth the average number of pulses in a minute is	150
Just after birth	from 140 to 130
During the first year	130 to 115
During the second year	115 to 100
During the third year	100 to 90
About the seventh year	90 to 85
About the fourteenth year, the average number of pulses in a minute is from	85 to 80
In adult age	80 to 70
In old age	70 to 60
In decrepitude	75 to 65

Temperament and Sex.—In persons of sanguine temperament, the heart acts somewhat more frequently than in those of the phlegmatic ; and in the female sex more frequently than in the male.

Food and Drink. Exercise.—After a meal its action is accelerated, and still more so during bodily exertion or mental excitement ; it is slower during sleep.

Diurnal Variation.—It appears that, in the state of health, the pulse is most frequent in the morning, and becomes gradually slower as the day advances : and that this diminution of frequency is both more regular and more rapid in the evening than in the morning.

Posture.—It is found that, as a general rule, the pulse, especially in the adult male, is more frequent in the standing than in the sitting posture, and in the latter than in the recumbent position ; the difference being greatest between the standing and the sitting posture. The effect of change of posture is greater as the frequency of the pulse is greater, and, accordingly, is more marked in the morning than in the evening. By supporting the body in different postures, without the aid of muscular effort of the individual, it has been proved that the increased frequency of the pulse in the sitting and standing positions is dependent upon the muscular exertion engaged in maintaining them ; the usual effect of these postures on the pulse being almost entirely prevented when the usually attendant muscular exertion was rendered unnecessary. (Guy.)

Atmospheric Pressure.—The frequency of the pulse increases in a corresponding ratio with the elevation above the sea.

Temperature.—The rapidity and force of the heart's contractions are largely influenced by variations of temperature. The frog's heart, when excised, ceases to beat if the temperature be reduced to 32° F. (0° C.). When heat is gradually applied to it, both the speed and force of the heart's contractions increase till they reach a maximum. If the temperature is still further raised, the beats become irregular and feeble, and the heart at length stands still in a condition of "heat-rigor."

Similar effects are produced in warm-blooded animals. In the rabbit, the number of heart-beats is more than doubled when the temperature of the air was maintained at 105° F. (40°·5 C.). At 113°—114° F. (45° C.), the rabbit's heart ceases to beat.

Relative Frequency of the Pulse to that of Respiration.—In health there is observed a nearly uniform relation between the frequency of the pulse and of the respirations ; the proportion being, on an average, one respiration to three or four beats of the heart. The same relation is generally maintained in the cases in which the pulse is naturally accelerated, as after food or exercise ; but in disease this relation usually ceases. In many affections accompanied with increased frequency of the pulse, the respiration is, indeed, also accelerated, yet the degree of its acceleration may bear no definite proportion to the increased number of the heart's actions : and in many other cases, the pulse becomes more frequent without any accompanying increase in the number of respirations; or, the respiration alone may be accelerated, the number of pulsations remaining stationary, or even falling below the ordinary standard.

The Force of the Ventricular Systole and Diastole.—The *force* of the left ventricular systole is more than double that exerted by the contraction of the right: this difference in the amount of force exerted by the contraction of the two ventricles, results from the walls of the left ventricle being about twice or three times as thick as those of the right. And the difference is adapted to the greater degree of resistance which the left ventricle has to overcome, compared with that to be overcome by the right: the former having to propel blood through every part of the body, the latter only through the lungs.

The actual amount of the intra-ventricular pressures during systole in the dog has been found to be 2·4 inches (60 mm.) of mercury in the right ventricle, and 6 inches (150 mm.) in the left. During diastole there is in the right ventricle a negative or suction pressure of about $\frac{2}{3}$ of an inch (– 17 to – 16 mm.), and in the left ventricle from 2 inches to $\frac{4}{5}$ of an inch (— 52 to — 20 mm.). Part of this fall in pressure, and possibly the greater part, is to be referred to the influence of respiration; but without this the negative pressure of the left ventricle caused by its active dilatation is about $\frac{4}{5}$ of an inch (23 mm.) of mercury.

The right ventricle is undoubtedly aided by this suction power of the left, so that the whole of the work of conducting the pulmonary circulation does not fall upon the right side of the heart, but is assisted by the left side.

The Force of the Auricular Systole and Diastole.—The maximum pressure within the right auricle is about $\frac{4}{5}$ of an inch (20 mm.) of mercury, and is probably somewhat less in the left. It has been found that during diastole the pressure within both auricles sinks considerably below that of the atmosphere; and as some fall in pressure takes place, even when the thorax of the animal operated upon has been opened, a certain proportion of the fall must be due to active auricular dilatation independent of respiration. In the right auricle, this negative pressure is about — 10 mm.

Work Done by the Heart.—In estimating the work done by any machine it is usual to express it in terms of the "unit of work." The unit of work is defined to be the energy expended in raising a unit of weight (1 lb.) through a unit of height (1 ft.). In England, the unit of work is the "*foot-pound*," in France, the "*kilogrammetre*."

The work done by the heart at each contraction can be readily found by multiplying the weight of blood expelled by the ventricles by the height to which the blood rises in a tube tied into an artery. This height was found to be about 9 ft. in the horse, and the estimate is nearly correct for a large artery in man. Taking the weight of blood expelled from the left ventricle at each systole as 6 oz., *i.e.*, $\frac{3}{8}$ lb., we have $9 \times \frac{3}{8} = 3{\cdot}375$ foot-pounds as the work done by the left ventricle at each systole; and adding to this the work done by the right ventricle (about one-third that of the left) we have $3{\cdot}375 \times 1{\cdot}125 = 4{\cdot}5$ foot-pounds as the work done by the heart at each contraction. Other estimates give $\frac{1}{2}$ kilogrammetre, or about $3\frac{1}{2}$ foot-pounds. Haughton estimates the total work of the heart in 24 hours as about 124 foot-tons.

Influence of the Nervous System on the Action of the Heart.—The hearts of warm-blooded animals cease to beat almost if not quite immediately after removal from the body, and are, therefore, unfavourable for the study of the nervous mechanism which regulates their action. Observations have, hitherto, therefore, been principally directed to the heart of cold-blooded animals, *e.g.*, the frog, tortoise, and snake, which will continue to beat under favourable conditions for many hours after removal from the body. Of these animals, the frog is the one mostly employed, and, indeed, until recently, it was from the study of the frog's heart that the chief part of our information was obtained. If removed from the body entire, the frog's heart will continue to beat for many hours and even days, and the beat has no apparent difference from the beat of the heart before removal from the body; it will take place without the presence of blood or other fluid within its chambers. If the beats have become infrequent, an additional beat may be induced by stimulating the heart by means of a blunt needle; but the time before the stimulus applied produces its result (the latent period) is very prolonged, and as in this way the cardiac beat is like the contraction of unstriped muscle, the method has been likened to a peristaltic contraction.

There is much uncertainty about the nervous mechanism of the beat of the frog's heart, but what has just been said shows, at any rate, two things; firstly, that as the heart will beat when removed from the body in a way differing not at all from the normal, it must contain within itself the mechanism of rhythmical contraction; and secondly, that as it can beat without the presence of fluid within its chambers, the movement cannot depend merely on reflex excitation by the entrance of blood. The nervous apparatus existing in the heart itself consists of collections of microscopic ganglia, and of nerve-fibres proceeding from them. These ganglia are demonstrable as being collected chiefly into three groups; one is in the wall of the sinus venosus (Remak's); a second, near the junction between the auricle and ventricle (Bidder's); and the third in the septum between the auricles.

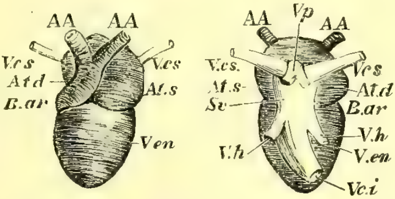

Fig. 106.—*Heart of frog.* (Burdon-Sanderson after Fritsche.) Front view to the left, back view to the right. *A A.* Aortæ. *V. cs.* Venæ cavæ superiores. At *s*, left auricle. At *d*, right auricle. *Ven.*, ventricle. *B. ar*, Bulbus arteriosus. *S. v.*, Sinus venosus. *V. c. i.*, Vena cava inferior. *V. h.*, Venæ hepaticæ. *V. p.*, Venæ pulmonales.

Some very important experiments seem to identify the rhythmical contractions of the frog's heart with these ganglia. If the heart be removed entire from the body, the sequence of the contraction of its several beats will take place with rhythmical regularity, viz., of the sinus venosus, the auricles, the ventricle, and bulbus arteriosus, in order. If the heart be removed at the junction of the sinus and auricle, the former will continue to beat, but the removed portion will for a short variable time stop beating, and then resume its beats, but with a rhythm different to that of the sinus: and, further, if the ventricle be removed, it will take a still longer time before recommencing its pulsation after its removal than the larger portion consisting of the auricles and ventricle, and its rhythm is different from that of the unremoved portion, and not so regular, nor will it continue to pulsate so long: during the period of stoppage a contraction will occur if the ventricle be mechanically or otherwise stimulated. If the lower two-thirds or apex of the ventricle be removed, the remainder of the heart will go on beating regularly in the body, but this part will remain motionless, and will not beat spontaneously, although it will respond to stimuli. If the heart be divided lengthwise, its parts will continue to pulsate rhythmically, and the auricles may be cut up into pieces, and the pieces will continue their movements of contraction. It will be thus seen that the rhythmical movements appear to be more marked in the parts supplied by the ganglia, and that the apical portion of the ventricle, in which the ganglia are not found, does not possess the power of automatic movement. Although the theory that the pulsations of the rest of the heart are dependent upon that of the sinus, and to stimuli proceeding from it, when connection is maintained, and only to reflex stimuli when removal has taken place, cannot be absolutely upheld, yet it is evident that the power of spontaneous contraction is strongest in the sinus, less strong in the auricles, and less so still in the ventricle, and that, therefore, the sinus ganglia are probably important in exciting the rhythmical contraction of the whole heart. This is expressed in the following way:—"The power of independent rhythmical contraction decreases regularly as we pass from the sinus to the ventricles," and "The rhythmical power of each segment of the heart varies inversely as its distance from the sinus." (Gaskell.)

It has been recently shown that, under appropriate stimuli, even the extreme apex of the ventricle in the tortoise may take on rhythmical contractions, or in other words may be "taught to beat" rhythmically. (Gaskell.)

Inhibition of the Heart's Action.—Although, under ordinary conditions, the apparatus of ganglia and nerve-fibres in the substance of the heart forms the medium through which its action is excited and rhythmically maintained, yet they, and, through them, the heart's contractions, are regulated by nerves which pass to them from the higher nerve-centres. These nerves are branches from the *pneumogastric* or *vagus* and the *sympathetic.*

The influence of the vagi nerves over the heart-beat may be shown by stimulating one (especially the right) or both of the nerves when a record is being taken of the beats of the frog's heart. If a single induction shock be sent into the nerve, the heart, after a short interval, ceases beating, but after the suppression of several beats resumes its action. As already mentioned, the effect of the stimulus is not immediately seen, and one beat may occur before the heart stops after the application of the electric-current. The stoppage of the heart may occur apparently in one of two ways, either by diminution of the strength of the systole or by increasing the length of the diastole. The stoppage of the heart may be brought about by the application of the electrodes to any part of the vagus, but most effectually if they are applied near the position of Remak's ganglia. It is supposed that the fibres of the vagi, therefore, terminate there in *inhibitory* ganglia in the heart-walls, and that the inhibition of the heart's beats, by means of the vagus, is not a simple action, but that it is produced by stimulating centres in the heart itself. These inhibitory centres are paralyzed by atropin, and then no amount of stimulation of the vagus, or of the heart itself, will produce any effect upon the cardiac beats. Urari in large doses paralyzes the vagus fibres, but in this case, as the inhibitory action can be produced by direct stimulation of the heart, it is inferred that this drug does not paralyze the ganglia themselves. Muscarin and pilocarpin appear to produce effects similar to those obtained by stimulating the vagus fibres.

If a ligature be tightly tied round the heart over the situation of the ganglia between the sinus and the auricles, the heart stops beating. This experiment (Stannius') would seem to stimulate the inhibitory ganglia, but for the remarkable fact that atropin does not interfere with its success. If the part (the ventricle) below the ligature be cut off, it will begin and continue to beat rhythmically; this may be explained by supposing that the stimulus of section induces pulsation in the part which is removed from the influence of the inhibitory ganglia.

So far, the effect of the terminal apparatus of the vagi has been considered; there is, however, reason for believing that the vagi nerves are simply the media of an *inhibitory* or restraining influence over the action of the heart, which is conveyed through them from a *centre* in the medulla oblongata which is always in operation, and, because of its restraining the heart's action, is called the *cardio-inhibitory* centre. For, on dividing these nerves, the pulsations of the heart are increased in frequency, an effect opposite to that produced by stimulation of their divided (peripheral) ends. The restraining influence of the centre in the medulla may be increased reflexly, producing slowing or stoppage of the heart, through influence passing from it down the vagi. As an example of the latter, the well-known effect on the heart of a violent blow on the epigastrium may be referred to. The stoppage of the heart's action is due to the conveyance of the stimulus by fibres of the sympathetic to the medulla oblongata, and its subsequent *reflection* through the vagi to the inhibitory ganglia of the heart. It is also believed that the power of the medullary inhibitory centre may be reflexly lessened, producing accelerated action of the heart.

Acceleration of Heart's Action.—Through certain fibres of the sympathetic, the heart receives an *accelerating* influence from the medulla oblongata. These accelerating nerve-fibres, issuing from the spinal cord in the neck, reach the inferior cervical ganglion, and pass thence to the cardiac plexus, and so to the heart. Their function is shown in the quickened pulsation which follows stimulation of the spinal cord, when the latter has been cut off from all connection with the heart, excepting that which is formed by the accelerating filaments from the inferior cervical ganglion. Unlike the inhibitory fibres of the pneumogastric, the accelerating fibres are not continuously in action.

The accelerator nerves must not, however, be considered as direct antagonists of the vagus; for if at the moment of their maximum stimulation, the vagus be stimulated with minimum currents, inhibition is produced with the same readiness as if these were not acting.

The connection of the heart with other organs by means of the nervous system, and the influences to which it is subject through them, are shown in a striking manner by the phenomena of disease. The influence of mental shock in arresting or modifying the action of the heart, the slow pulsation which accompanies compression of the brain, the irregularities and palpitations caused by dyspepsia or hysteria, are good evidence of the connection of the heart with other organs through the nervous system.

The action of the heart is no doubt also very materially affected by the nutrition of its walls by a sufficient supply of healthy blood sent to them, and it is not unlikely that the apparently contradictory effect of poisons may be explained by supposing that the influence of some of them is either partially or entirely directed to the muscular tissue itself, and not to the nervous apparatus alone. As will be explained presently, the heart exercises a considerable influence upon the condition of the pressure of blood within the arteries, but in its turn the blood-pressure within the arteries reacts upon the heart, and has a distinct effect upon its contractions, increasing by its increase, and *vice versâ*, the force of the cardiac beat, although the frequency is diminished as the blood-pressure rises. The quantity (and quality?) of the blood contained in each chamber, too, has an influence upon its systole, and within normal limits the larger the quantity the stronger the contraction. Rapidity of systole does not of necessity indicate strength, as two weak contractions often do no more work than one strong and prolonged. In order that the heart may do its maximum work, it must be allowed free space to act; for if obstructed in its action by mechanical outside pressure, as by an excess of fluid within the pericardium, such as is produced by inflammation, or by an overloaded stomach, or what not, the pulsations become irregular and feeble.

The Arteries.

Distribution.—The arterial system begins at the left ventricle in a single large trunk, the aorta, which almost immediately after its origin gives off in its course in the thorax three large branches for the supply of the head, neck, and upper extremities; it then traverses the thorax and abdomen, giving off branches, some large and some small, for the supply of the various organs and tissues it passes on its way. In the abdomen it divides into two chief branches, for the supply of the lower extremities. The arterial branches wherever given off divide and subdivide, until the calibre of each subdivision becomes very minute, and these minute vessels pass into capillaries. Arteries are, as a rule, placed in situations protected from pressure and other dangers, and are, with few exceptions, straight in their course, and frequently communicate with other arteries (anastomose or inosculate). The branches are usually given off at an acute angle, and the area of the branches of an artery generally exceeds that of the parent trunk; and as the distance from the origin is increased, the area of the combined branches is increased also.

After death, arteries are usually found dilated (not collapsed as the veins are) and empty, and it was to this fact that their name was given them, as the ancients believed that they conveyed air to the various parts of the body. As regards the arterial system of the lungs (pulmonary system) it begins at the right ventricle in the pulmonary artery, and is distributed much as the arteries belonging to the general systemic circulation.

Structure.—The walls of the arteries are composed of three principal coats, termed the *external* or *tunica adventitia*, the *middle* or *tunica media*, and the *internal* coat or *tunica intima.*

The *external coat* or *tunica adventitia* (figs. 107 and 111, *t. a.*), the strongest and toughest part of the wall of the artery, is formed of areolar tissue, with which is mingled throughout a network of elastic fibres. At the inner part of this outer coat the elastic network forms in most arteries so distinct a layer as to be sometimes called the *external elastic coat* (fig. 123, *e. e.*).

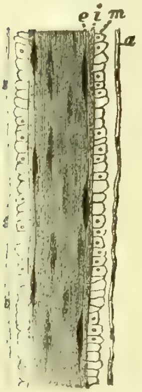

Fig. 107.—*Minute artery* viewed in longitudinal section. *e.* Nucleated endothelial membrane, with faint nuclei in lumen, looked at from above. *i.* Thin elastic tunica intima. *m.* Muscular coat or tunica media. *a.* Tunica adventitia. (Klein and Noble Smith.) × 250.

The *middle coat* (fig. 107, *m*) is composed of both muscular and elastic fibres, with a certain proportion of areolar tissue. In the larger arteries (fig. 110) its thickness is comparatively as well as absolutely much greater than in the small, constituting, as it does, the greater part of the arterial wall.

The muscular fibres, which are of the unstriped variety (fig. 109) are arranged for the most part transversely to the long axis of the artery (fig. 107, *m*); while the elastic element, taking also a transverse direction, is disposed in the form of closely interwoven and branching fibres, which intersect in all parts the layers of muscular fibre. In arteries of various size there is a difference in the proportion of the muscular and elastic element, elastic tissue preponderating in the largest arteries, while this condition is reversed in those of medium and small size.

The *internal coat* is formed by layers of elastic tissue, consisting in part of coarse longitudinal branching fibres, and in part of a very thin and brittle membrane which possesses little elasticity, and is thrown into folds or wrinkles when the artery contracts. This latter membrane, the striated or *fenestrated coat of Henle* (fig. 108), is peculiar in its tendency to curl up, when peeled off from the artery, and in the perforated and streaked appearance which it presents under the microscope. Its inner surface is lined with a delicate layer of endothelium, composed of elongated cells

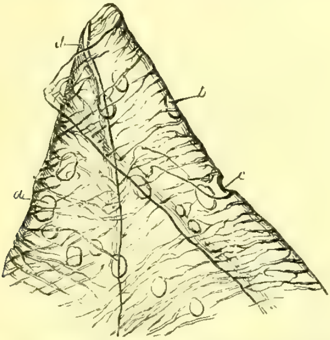

Fig. 108.—*Portion of fenestrated membrane* from the femoral artery. × 200. *a, b, c.* Perforations. (Henle.)

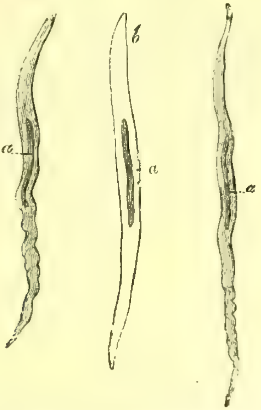

Fig. 109.—*Muscular fibre-cells from human arteries*, magnified 350 diameters. (Kölliker.) *a.* Nucleus. *b.* A fibre-cell treated with acetic acid.

(fig. 112, *a*), which make it smooth and polished, and furnish a nearly impermeable surface, along which the blood may flow with the smallest possible amount of resistance from friction.

Immediately external to the endothelial lining of the artery is fine connective tissue, *sub-endothelial layer*, with branched corpuscles. Thus the internal coat consists of three parts, (*a*) an endothelial lining, (*b*) the sub-endothelial layer, and (*c*) elastic layers.

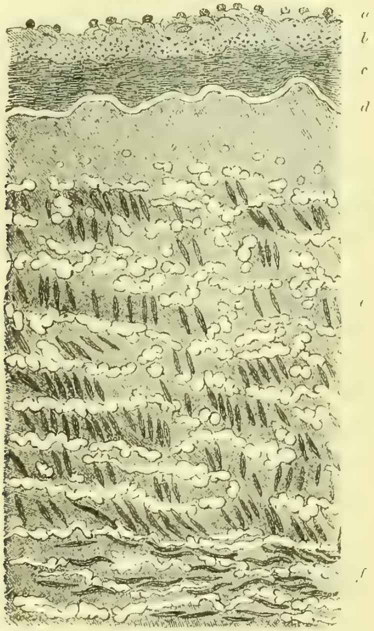

Fig. 110.—*Transverse section of aorta through internal and about half the middle coat. a.* Lining endothelium with the nuclei of the cells only shown. *b.* Subepithelial layer of connective tissue. *c*, *d*. Elastic tunica intima proper, with fibrils running circularly or longitudinally. *e*, *f*. Middle coat, consisting of elastic fibres arranged longitudinally, with muscle-fibres cut obliquely, or longitudinally. (Klein.)

Vasa Vasorum.—The walls of the arteries, with the possible exception of the endothelial lining and the layers of the internal coat immediately outside it, are not nourished by the blood which they convey, but are, like other parts of the body, supplied with little arteries, ending in capillaries and veins, which, branching throughout the external coat, extend for some distance into the middle, but do not reach the internal coat. These nutrient vessels are called *vasa vasorum.*

Lymphatics of Arteries and Veins.—Lymphatic spaces are present in the coats of both arteries and veins; but in the tunica adventitia or external coat of large vessels they form a distinct plexus of more or less tubular vessels. In smaller vessels they appear as sinous spaces lined by endothelium. Sometimes, as in the arteries of the omentum, mesentery, and membranes of the brain, in the pulmonary, hepatic, and splenic arteries, the spaces

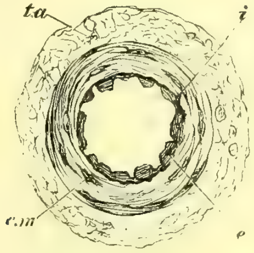

Fig. 111.—*Transverse section of small artery from soft palate.* *e*, endothelial lining, the nuclei of the cells are shown; *i*, elastic tissue of the intima, which is a good deal folded; *c. m.* circular muscular coat, showing nuclei of the muscle cells; *t. a.* tunica adventitia. × 300. (Schofield.)

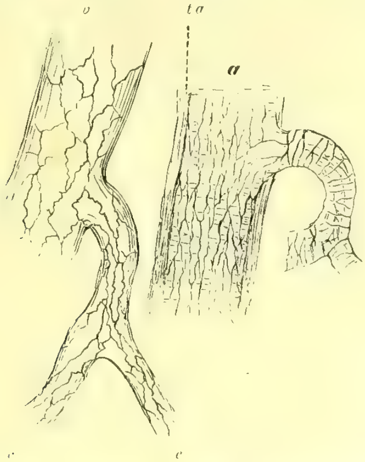

Fig. 112.—*Two blood-vessels from a frog's mesentery, injected with nitrate of silver, showing the outlines of the endothelial cells.* *a. Artery.* The endothelial cells are long and narrow; the transverse markings indicate the muscular coat. *t. a.* Tunica adventitia. *v. Vein,* Showing the shorter and wider endothelial cells with which it is lined. *c, c.* Two capillaries entering the vein. (Schofield.)

are continuous with vessels which distinctly ensheath them—*perivascular lymphatic sheaths* (fig. 121). Lymph channels are said to be present also in the tunica media.

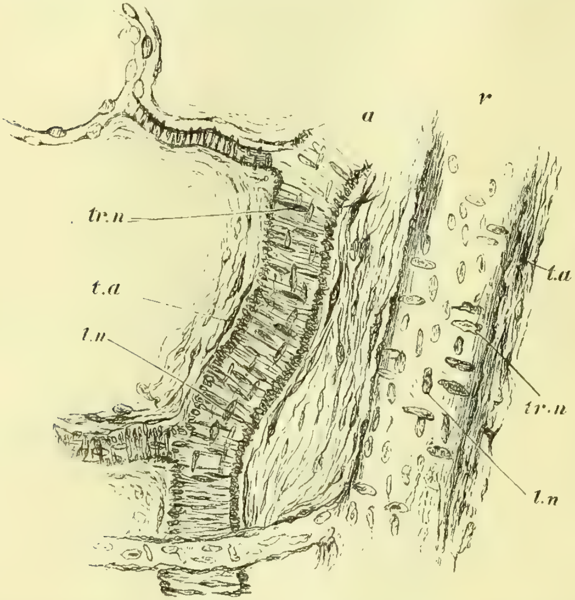

Fig. 113.—*Blood-vessels from mesocolon of rabbit.* *a. Artery*, with two branches, showing *tr. n.* nuclei of transverse muscular fibres; *l. n.* nuclei of endothelial lining; *t. a*: tunica adventitia. *v. Vein.* Here the transverse nuclei are more oval than those of the artery. The vein receives a small branch at the lower end of the drawing; it is distinguished from the artery among other things by its straighter course and larger calibre. c. Capillary, showing nuclei of endothelial cells. × 300. (Schofield.)

Nervi Vasorum.—Most of the arteries are surrounded by a plexus of sympathetic nerves, which twine around the vessel very much like ivy round a tree: and ganglia are found at frequent intervals. The smallest arteries and capillaries are also surrounded by a very delicate network of similar nerve-fibres, many of which appear to end in the nuclei of the transverse muscular fibres (fig. 122). It is through these plexuses that the calibre of the vessels is regulated by the nervous system (p. 190).

The Capillaries.

Distribution.—In all vascular textures, except some parts of the corpora cavernosa of the penis, and of the uterine placenta, and of the spleen, the transmission of the blood from the minute branches of the arteries to the minute veins is effected through a network of *microscopic* vessels, called *capillaries.* These may be seen in all minutely injected preparations; and during life, in any transparent vascular parts,—such as the web of the frog's foot, the tail or external branchiæ of the tadpole, or the wing of the bat.

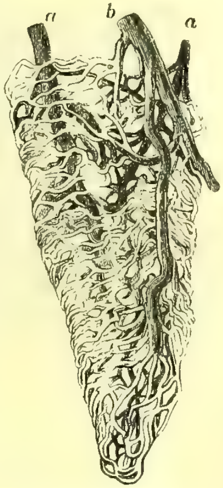

Fig. 114.—*Blood-vessels of an intestinal villus*, representing the arrangement of capillaries between the ultimate venous and arterial branches; *a*, *a*, the arteries; *b*, the vein.

The branches of the minute arteries form repeated anastomoses with each other, and give off the capillaries which, by their anastomoses, compose a continuous and uniform network, from which the venous radicles take their rise (fig. 114). The point at which the arteries terminate and the minute veins commence, cannot be exactly defined, for the transition is gradual; but the capillary network has, nevertheless, this peculiarity, that the small vessels which compose it maintain the same diameter throughout: they do not diminish in diameter in one direction, like arteries and veins; and the meshes of the network that they compose are more uniform in shape and size than those formed by the anastomoses of the minute arteries and veins.

Structure.—This is much more simple than that of the arteries or veins. Their walls are composed of a single layer of elongated or radiate, flattened and nucleated cells, so joined and dovetailed together as to form a continuous transparent membrane (fig. 115). Outside these cells, in the larger capillaries, there is a structureless, or very finely fibrillated membrane, on the inner surface of which they are laid down.

In some cases this external membrane is nucleated, and may then be regarded as a miniature representative of the tunica adventitia of arteries.

Here and there, at the junction of two or more of the delicate endothelial cells which compose the capillary wall, *pseudo-stomata* may be seen resembling those in serous membranes (p. 367).

The endothelial cells are often continuous at various points with processes of adjacent connective-tissue corpuscles.

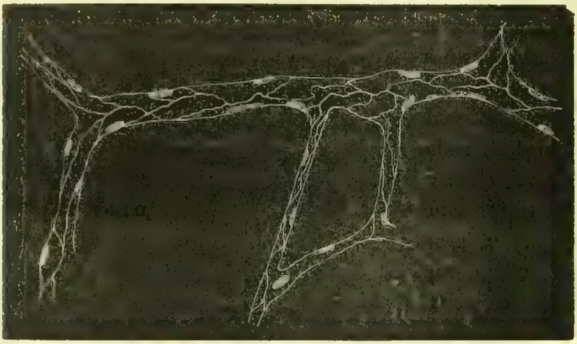

Fig. 115.—*Capillary blood-vessels from the omentum of rabbit*, showing the nucleated endothelial membrane of which they are composed. (Klein and Noble Smith.)

Capillaries are surrounded by a delicate nerve-plexus resembling, in miniature, that of the larger blood-vessels.

The *diameter* of the capillary vessels varies somewhat in the different textures of the body, the most common size being about $\frac{1}{3000}$th of an inch. Among the smallest may be mentioned those of the brain, and of the follicles of the mucous membrane of the intestines; among the largest, those of the skin, and especially those of the medulla of bones.

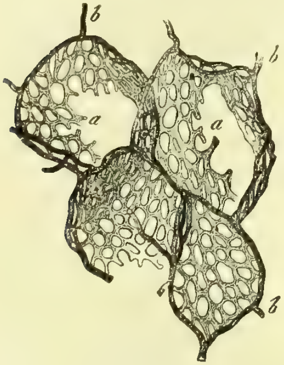

Fig. 116.—*Network of capillary vessels of the air-cells of the horse's lung magnified.* *a*, *a*, capillaries proceeding from *b*, *b*, terminal branches of the pulmonary artery. (Frey.)

The *size* of capillaries varies necessarily in different animals in relation to the size of their blood corpuscles: thus, in the Proteus, the capillary circulation can just be discerned with the naked eye.

The *form* of the capillary network presents considerable variety in the different textures of the body: the varieties consisting principally of modifications of two chief kinds of mesh, the rounded and the elongated. That kind of which the meshes or interspaces have a roundish form is the most common, and prevails in those parts in which the capillary network is most dense, such as the lungs (fig. 116), most glands, and mucous membranes, and the cutis. The meshes of this kind of network are not quite circular but more or less angular, sometimes presenting a nearly regular quadrangular or polygonal form, but being more frequently irregular. The capillary network with elongated meshes (fig. 117) is observed in parts in which the vessels are arranged among bundles of fine tubes or fibres, as in muscles and nerves. In such parts, the meshes usually have the form of a parallelogram, the short sides of which may be from three to eight or ten times less than the long ones; the long sides always corresponding to the axis of the fibre or tube, by which it is placed. The appearance of both the rounded and elongated meshes is much varied according as the vessels composing them have a straight or tortuous form. Sometimes the capillaries have a looped arrangement, a single capillary projecting from the common network into some prominent organ, and returning after forming one or more loops, as in the papillæ of the tongue and skin.

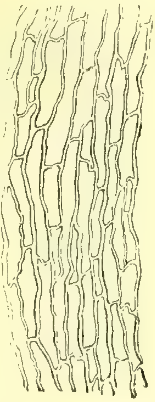

Fig. 117.—*Injected capillary vessels of muscle seen with a low magnifying power.* (Sharpey.)

The *number* of the capillaries and the *size of the meshes* in different parts determine in general the degree of *vascularity* of those parts. The parts in which the network of capillaries is closest, that is, in which the meshes or interspaces are the smallest, are the lungs and the choroid membrane of the eye. In the iris and ciliary body, the interspaces are somewhat wider, yet very small. In the human liver the interspaces are of the same size, or even smaller than the capillary vessels themselves. In the human lung they are smaller than the vessels; in the human kidney, and in the kidney of the dog, the diameter of the injected capillaries, compared with that of the interspaces, is in the proportion of one to four, or of one to three. The brain receives a very large quantity of blood; but the capillaries in which the blood is distributed through its substance are very minute, and less numerous than in some other parts. Their diameter, according to E. H. Weber, compared with the long diameter of the meshes, being in the proportion of one to eight or ten; compared with the transverse diameter, in the proportion of one to four or six. In the mucous membranes—for example in the conjunctiva and in the cutis vera, the capillary vessels are much larger than in the brain, and the interspaces narrower,—namely, not more than three or four times wider than the vessels. In the periosteum the meshes are much larger. In the external coat of arteries, the width of the meshes is ten times that of the vessels (Henle).

It may be held as a general rule, that the more active the functions of an organ are, the more vascular it is. Hence the narrowness of the interspaces in all glandular organs, in mucous membranes, and in growing parts; their much greater width in bones, ligaments, and other very tough and comparatively inactive tissues; and the usually complete absence of vessels in cartilage, and such parts as those in which, probably, very little *vital* change occurs after they are once formed.

The Veins.

Distribution.—The venous system begins in small vessels which are slightly larger than the capillaries from which they spring. These vessels are gathered up into larger and larger trunks until they terminate (as regards the systemic circulation) in the two venæ cavæ and the coronary veins, which enter the right auricle, and (as regards the pulmonary circulation) in four pulmonary veins, which enter the left auricle. The capacity of the veins diminishes as they approach the heart; but, as a rule, the capacity of the veins exceeds by several times (twice or three times) that of their corresponding arteries. The pulmonary veins, however, are an exception to this rule, as they do not exceed in capacity the pulmonary arteries. The veins are found after death as a rule to be more or less collapsed, and often to contain blood. The veins are usually distributed in a superficial and a deep set which communicate frequently in their course.

Structure.—In structure the coats of veins bear a general resemblance to those of arteries (fig. 118). Thus, they possess an *outer*, *middle*, and *internal* coat. The *outer* coat is constructed of areolar tissue like that of the arteries, but is thicker. In some veins it contains muscular fibre-cells, which are arranged longitudinally.

The *middle* coat is considerably thinner than that of the arteries; and, although it contains circular unstriped muscular fibres or fibre-cells, these are mingled with a larger proportion of yellow elastic and white fibrous tissue. In the large veins, near the heart, namely the *venæ cavæ* and pulmonary veins, the middle coat is replaced, for some distance from the heart, by circularly arranged striped muscular fibres, continuous with those of the auricles.

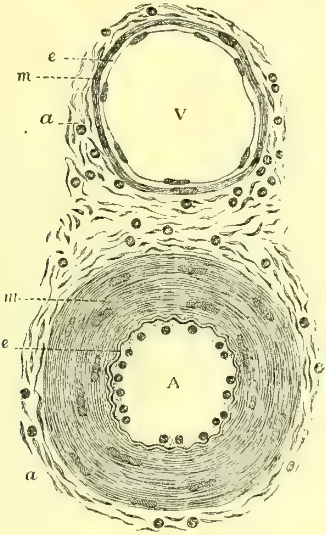

Fig. 118.—*Transverse section through a small artery and vein* of the mucous membrane of a child's epiglottis: the contrast between the thick-walled artery and the thin-walled vein is well shown. A. Artery, the letter is placed in the lumen of the vessel. *e.* Endothelial cells with nuclei clearly visible: these cells appear very thick from the contracted state of the vessel. Outside it a double wavy line marks the elastic tunica intima. *m.* Tunica media forming the chief part of arterial wall and consisting of unstriped muscular fibres circularly arranged: their nuclei are well seen. *a.* Part of the tunica adventitia showing bundles of connective-tissue fibres in section, with the circular nuclei of the connective-tissue corpuscles. This coat gradually merges into the surrounding connective-tissue. V. In the lumen of the vein. The other letters indicate the same as in the artery. The muscular coat of the vein (*m*) is seen to be much thinner than that of the artery. × 350. (Klein and Noble Smith.)

The *internal* coat of veins is less brittle than the corresponding coat of an artery, but in other respects resembles it closely.

Valves.—The chief influence which the veins have in the circulation, is effected with the help of the *valves*, which are placed in all veins subject to local pressure from the muscles between or near which they run. The general construction of these valves is similar to that of the semilunar valves of the aorta and pulmonary artery, already described; but their free margins are turned in the opposite direction, *i.e.*, *towards* the heart, so as to stop any movement of blood backward in the veins. They are commonly placed in pairs, at various distances in different veins, but almost uniformly in each (fig. 119). In the smaller veins, single valves are often met with; and three or four are sometimes placed together, or near one another, in the largest veins, such as the subclavian, and at their junction with the jugular veins. The valves are semilunar; the unattached edge being in some examples concave, in others straight. They are composed of inextensile fibrous tissue, and are covered with endothelium like that lining the veins. During the period of their inaction, when the venous blood is flowing in its proper direction, they lie by the sides of the veins; but when in action, they close together like the valves of the arteries, and offer a complete barrier to any backward movement of the blood (figs. 119 and 120). Their situation in the superficial veins of the forearm is readily discovered by pressing along its surface, in a direction opposite to the venous current, *i. e.*, from the elbow towards the wrist; when little swellings

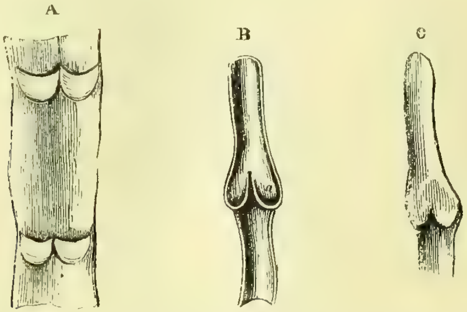

Fig. 119.—*Diagram showing valves of veins.* A, part of a vein laid open and spread out, with two pairs of valves. B. longitudinal section of a vein, showing the apposition of the edges of the valves in their closed state. C, portion of a distended vein, exhibiting a swelling in the situation of a pair of valves.

(fig. 119, c) appear in the position of each pair of valves. These swellings at once disappear when the pressure is relaxed.

Valves are not equally numerous in all veins, and in many they are absent altogether. They are most numerous in the veins of the extremities, and more so in those of the leg than the arm. They are commonly *absent* in veins of less than a line in diameter, and, as a general rule, there are few or none in those which are not subject to muscular pressure. Among those veins which have no valves may be mentioned the superior and inferior vena cava, the trunk and branches of the portal vein, the hepatic and renal veins, and the pulmonary veins; those in the interior of the cranium and vertebral column, those of the bones, and the trunk and branches of the umbilical vein are also destitute of valves.

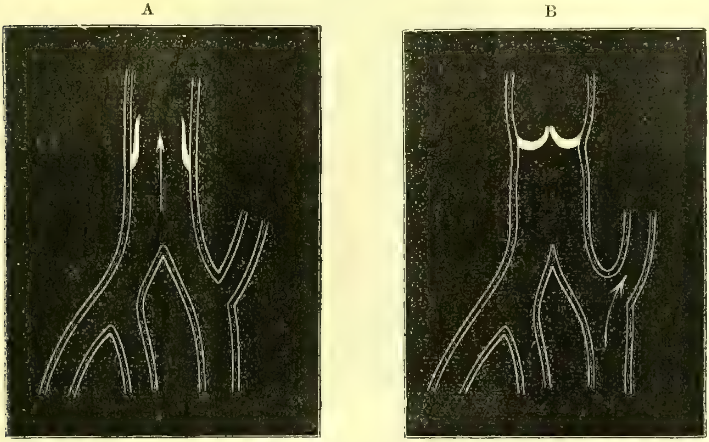

Fig. 120.—A, *vein with valves open.* B, *vein with valves closed:* stream of blood passing off by lateral channel. (Dalton.)

Circulation in the Arteries.

Functions of the External Coat of Arteries.—The external coat forms a strong and tough investment, which, though capable of extension, appears principally designed to strengthen the arteries and to guard against their excessive distension by the force of the heart's action. It is this coat which alone prevents the complete severance of an artery when a ligature is tightly applied; the internal and middle coats being divided. In it, too, the little *vasa vasorum* (p. 162) find a suitable tissue in which to subdivide for the supply of the arterial coats.

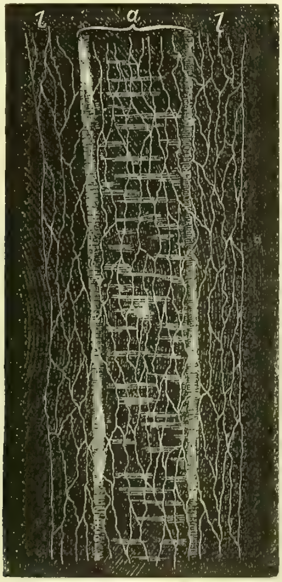

Fig. 121.—*Surface view of an artery from the mesentery of a frog*, ensheathed in a perivascular lymphatic vessel. *a*. The artery, with its circular muscular coat (media) indicated by broad transverse markings, with an indication of the adventitia outside. *l*. Lymphatic vessel; its wall is a simple endothelial membrane. (Klein and Noble Smith.)

Functions of the Elastic Tissue in Arteries.—The purpose of the elastic tissue, which enters so largely into the formation of all the coats of the arteries, is, (*a*) to guard the arteries from the suddenly exerted pressure to which they are subjected at each contraction of the ventricles. In every such contraction, the contents of the ventricles are forced into the arteries more quickly than they can be discharged into and through the capillaries. The blood therefore, being, for an instant, resisted in its onward course, a part of the force with which it was impelled is directed against the sides of the arteries; under this force their elastic walls dilate, stretching enough to receive the blood, and as they stretch, becoming more tense and more resisting. Thus, by yielding, they break the shock of the force impelling the blood. On the subsidence of the pressure, when the ventricles cease contracting, the arteries are able, by the same elasticity, to resume their former calibre; (*b.*) It equalizes the current of the blood by maintaining pressure on it in the arteries during the periods at which the ventricles are at rest or dilating. If the arteries had been rigid tubes, the blood, instead of flowing, as it does, in a constant stream, would have been propelled through the arterial system in a series of jerks corresponding to the ventricular contractions, with intervals of almost complete rest during the inaction of the ventricles. But in the actual condition of the arteries, the force of the successive contractions of the ventricles is expended partly in the direct propulsion of the blood, and partly in the dilatation of the elastic arteries; and in the intervals between the contractions of the ventricles, the force of the recoil is employed in continuing the same direct propulsion. Of course, the pressure they exercise is equally diffused in every direction, and the blood tends to move backwards as well as onwards, but all movement backwards is prevented by the closure of the semi-lunar arterial valves (p. 141), which takes place at the very commencement of the recoil of the arterial walls.

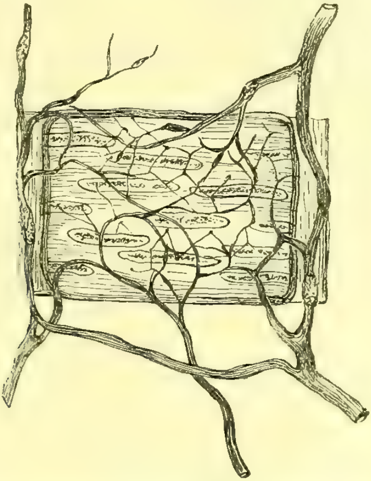

Fig. 122.—*Ramification of nerves* and termination in the muscular coat of a small artery of the frog (Arnold).

By this exercise of the elasticity of the arteries, all the force of the ventricles is made advantageous to the circulation; for that part of their force which is expended in dilating the arteries, is restored in full when they recoil. There is thus no loss of force; but neither is there any gain, for the elastic walls of the artery cannot originate any force for the propulsion of the blood—they only restore that which they received from the ventricles. The force with which the arteries are dilated every time the ventricles contract, might be said to be received by them in store, to be all given out again in the next succeeding period of dilatation of the ventricles. It is by this equalizing influence of the successive branches of every artery that, at length, the intermittent accelerations produced in the arterial current by the action of the heart, cease to be observable, and the jetting stream is converted into the continuous and equable movement of the blood which we see in the capillaries and veins. In the production of a continuous stream of blood in the smaller arteries and capillaries, the resistance which is offered to the blood-stream in these vessels (p. 197), is a necessary agent. Were there no greater obstacle to the *escape* of blood from the larger arteries than exists to its *entrance* into them from the heart, the stream would be intermittent, notwithstanding the elasticity of the walls of the arteries.

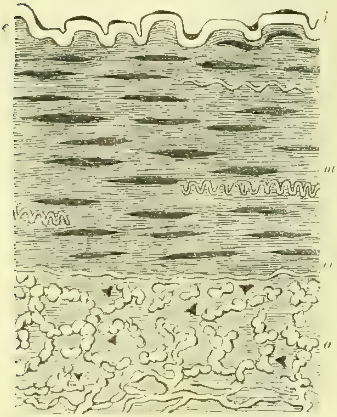

Fig. 123.—*Transverse section* through a large branch of the inferior mesenteric artery of a pig. *e*, endothelial membrane; *i*, tunica elastica interna, no subendothelial layer is seen; *m*, muscular tunica media, containing only a few wavy elastic fibres; *ee*, tunica elastica externa, dividing the media from the connective tissue adventitia, *a*. (Klein and Noble Smith.) × 350.

(*c*.) By means of the elastic tissue in their walls (and of the muscular tissue also), the arteries are enabled to dilate and contract readily in correspondence with any temporary increase or diminution of the total quantity of blood in the body; and within a certain range of diminution of the quantity, still to exercise due pressure on their contents; (*d*.) The elastic tissue assists in restoring the normal state after *diminution* of its calibre, whether this has been caused by a contraction of the muscular coat, or the temporary application of a compressing force from without. This action is well shown in arteries which, having contracted by means of their muscular element, after death, regain their average patency on the cessation of post-mortem rigidity (p. 177). (*e.*) By means of their elastic coat the arteries are enabled to adapt themselves to the different movements of the several parts of the body.

Tension of Arteries.—The natural state of all arteries, in regard at least to their length, is one of tension—they are always more or less stretched, and ever ready to recoil by virtue of their elasticity, whenever the opposing force is removed. The extent to which the divided extremities of arteries retract is a measure of this tension, not of their elasticity. (Savory.)

Functions of the Muscular Coat.—The most important office of the *muscular* coat is, (1) that of regulating the quantity of blood to be received by each part or organ, and of adjusting it to the requirements of each, according to various circumstances, but, chiefly, according to the activity with which the functions of each are at different times performed. The amount of work done by each organ of the body varies at different times, and the variations often quickly succeed each other, so that, as in the brain, for example, during sleep and waking, within the same hour a part may be now very active and then inactive. In all its active exercise of function, such a part requires a larger supply of blood than is sufficient for it during the times when it is comparatively inactive. It is evident that the heart cannot regulate the supply to each part at different periods; neither could this be regulated by any general and uniform contraction of the arteries; but it may be regulated by the power which the arteries of each part have, in their muscular tissue, of contracting so as to diminish, and of passively dilating or yielding so as to permit an increase of the supply of blood, according to the requirements of the part to which they are distributed. And thus, while the ventricles of the heart determine the total quantity of blood, to be sent onwards at each contraction, and the force of its propulsion, and while the large and merely elastic arteries distribute it and equalise its stream, the smaller arteries, in addition, regulate and determine, by means of their muscular tissue, the proportion of the whole quantity of blood which shall be distributed to each part.

It must be remembered, however, that this regulating function of the arteries is itself governed and directed by the nervous system (vaso-motor centres and fibres).

Another function of the muscular element of the middle coat of arteries is (2), to co-operate with the elastic in adapting the calibre of the vessels to the quantity of blood which they contain. For the amount of fluid in the blood-vessels varies very considerably even from hour to hour, and can never be quite constant; and were the elastic tissue only present, the pressure exercised by the walls of the containing vessels on the contained blood would be sometimes very small, and sometimes inordinately great. The presence of a muscular element, however, provides for a certain uniformity in the amount of pressure exercised; and it is by this adaptive, uniform, gentle, muscular contraction, that the normal *tone* of the blood-vessels is maintained. Deficiency of this *tone* is the cause of the soft and yielding pulse, and its unnatural excess, of the hard and tense one.

The elastic and muscular contraction of an artery may also be regarded as fulfilling a natural purpose when (3), the artery being cut, it first limits and then, in conjunction with the coagulated fibrin, arrests the escape of blood. It is only in consequence of such contraction and coagulation that we are free from danger through even very slight wounds; for it is only when the artery is closed that the processes for the more permanent and secure prevention of bleeding are established.

(4) There appears no reason for supposing that the muscular coat assists, to more than a very small degree, in propelling the onward current of blood.

(1.) When a small artery in the living subject is exposed to the air or cold, it gradually but manifestly contracts. Hunter observed that the posterior tibial artery of a dog when laid bare, became in a short time so much contracted as almost to prevent the transmission of blood; and the observation has been often and variously confirmed. Simple elasticity could not effect this.

(2.) When an artery is cut across, its divided ends contract, and the orifices may be completely closed. The rapidity and completeness of this contraction vary in different animals; they are generally greater in young than in old animals; and less, apparently, in man than in the lower animals. This contraction is due in part to elasticity, but in part, also, to muscular action; for it is generally increased by the application of cold, or of any simple stimulating substances, or by mechanically irritating the cut ends of the artery, as by picking or twisting them.

(3.) The contractile property of arteries continues many hours after death, and thus affords an opportunity of distinguishing it from their elasticity. When a portion of an artery of a recently killed animal is exposed, it gradually contracts, and its canal may be thus completely closed: in this contracted state it remains for a time, varying from a few hours to two days: then it dilates again, and permanently retains the same size.

This persistence of the contractile property after death was well shown in an observation of Hunter, which may be mentioned as proving, also, the greater degree of contractility possessed by the smaller than by the larger arteries. Having injected the uterus of a cow, which had been removed from the animal upwards of twenty-four hours, he found, after the lapse of another day, that the larger vessels had become much more turgid than when he injected them, and that the smaller arteries had contracted so as to force the injection back into the larger ones.

The Pulse.

If one extremity of an elastic tube be fastened to a syringe, and the other be so constricted as to present an obstacle to the escape of fluid, we shall have a rough model of what is present in the living body:—The syringe representing the heart, the elastic tube the arteries, and the contracted orifice the arterioles (smallest arteries) and capillaries. If the apparatus be filled with water, and if a finger-tip be placed on any part of the elastic tube, there will be felt with every action of the syringe, an impulse or beat, which corresponds exactly with what we feel in the arteries of the living body with every contraction of the heart, and call the *pulse*. The pulse is essentially caused by an expansion *wave*, which is due to the injection of blood into an already full aorta; which blood expanding the vessel produces the pulse in it, almost coincidently with the systole of the left ventricle. As the force of the left ventricle, however, is not expended in dilating the aorta only, the wave of blood passes on, expanding the arteries as it goes, running as it were on the surface of the more slowly travelling blood already contained in them, and producing the pulse as it proceeds.

The distension of each artery increases both its length and its diameter. In their elongation, the arteries change their form, the straight ones becoming slightly curved, and those already curved becoming more so, but they recover their previous form as well as their diameter when the ventricular contraction ceases, and their elastic walls recoil. The increase of their curves which accompanies the distension of arteries, and the succeeding recoil, may be well seen in the prominent temporal artery of an old person. In feeling the pulse, the finger cannot distinguish the sensation produced by the dilatation from that produced by the elongation and curving; that which it perceives most plainly, however, is the dilatation, or return, more or less, to the cylindrical form, of the artery which has been partially flattened by the finger.

The pulse—due to any given beat of the heart—is not perceptible at the same moment in all the arteries of the body. Thus,—it can be felt in the carotid a very short time before it is perceptible in the radial artery, and in this vessel again before the dorsal artery of the foot. The delay in the beat is in proportion to the distance of the artery from the heart, but the difference in time between the beat of any two arteries never exceeds probably $\frac{1}{6}$ to $\frac{1}{8}$ of a second.

A distinction must be carefully made between the passage of the *wave* along the arteries, and the velocity of the *stream* (p. 206) of blood. Both wave and current are present; but the rates at which they travel are very different; that of the wave 16·5 to 33 feet per second (5 to 10 metres), being twenty or thirty times as great as that of the current.

The Sphygmograph.—A great deal of light has been thrown on what may be called the form of the pulse by the sphygmograph (figs. 124 and 125). The principle on which the sphygmograph acts is very simple (see fig. 124). The small button replaces the finger in the act of taking the pulse, and is made to rest lightly on the artery, the pulsations of which it is desired to investigate. The up-and-down movement of the button is communicated to the lever, to the hinder end of which is attached a slight spring, which allows the lever to move up, at the same time that it is just strong enough to resist its making any sudden jerk, and in the interval of the beats also to assist in bringing it back to its original position. For ordinary purposes the instrument is bound on the wrist (fig. 125).

It is evident that the beating of the pulse with the reaction of the spring will cause an up-and-down movement of the lever, the pen of which will write the effect on a smoked card, which is made to move by clockwork in the direction of the arrow. Thus a tracing of the pulse is obtained, and in this way much more delicate effects can be seen, than can be felt on the application of the finger.

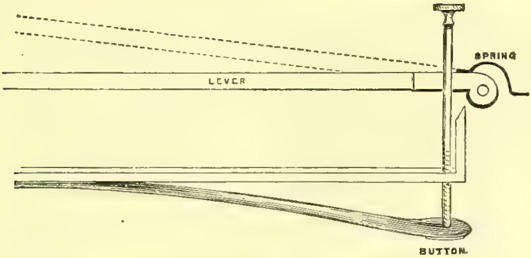

Fig. 124.—*Diagram of the mode of action of the Sphygmograph.*

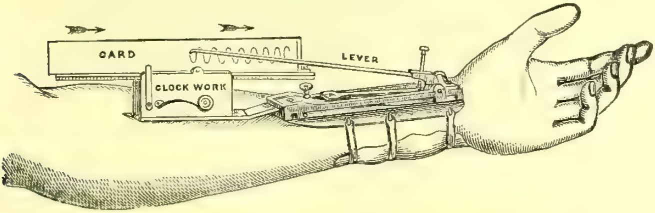

Fig. 125.—*The Sphygmograph* applied to the arm.

The pulse-tracing differs somewhat according to the artery upon which the sphygmograph is applied, but its general characters are much the same in all cases. It consists of :—A sudden upstroke (fig. 126, A), which is somewhat higher and more abrupt in the pulse of the carotid and of other arteries near the heart than in the radial and other arteries more remote ; and a gradual decline (B), less abrupt, and therefore taking a longer time than (A). It is seldom, however, that the decline is an uninterrupted fall ; it is usually marked about half-way by a distinct notch (C), called the *dicrotic notch*, which is caused by a second more or less marked ascent of the lever at that point by a second wave called the *dicrotic wave* (D) ; not unfrequently (in which case the tracing is said to have a double apex) there is also soon after the commencement of the descent a slight ascent previous to the dicrotic notch, this is called the *predicrotic wave* (C), and in addition there may be one or more slight ascents after the dicrotic, called *post dicrotic* (E).

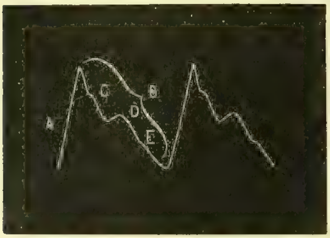

Fig. 126.—*Diagram of pulse-tracing.* A, upstroke; B, down-stroke; C, predicrotic wave; D, dicrotic; E, post dicrotic wave.

The explanation of these tracings presents some difficulties, not, however, as regards the two primary factors, viz., the upstroke and downstroke, because they are universally taken to mean the sudden injection of blood into the already full arteries, and that this passes through the artery as a wave and expands them, the gradual fall of the lever signifying the recovery of the arteries by their recoil. It may be demonstrated on a system of elastic tubes, such as was described above, where a syringe pumps in water at regular intervals, just as well as on the radial artery, or on a more complicated system of tubes in which the heart, the arteries, the capillaries and veins are represented, which is known as an *arterial schema.* If we place two or more sphygmographs upon such a system of tubes at increasing distances from the pump, we may demonstrate that the rise of the lever commences first in that nearest the pump, and is higher and more sudden, while at a longer distance from the pump the wave is less marked, and a little later. So in the arteries of the body the wave of blood gradually gets less and less as we approach the periphery of the arterial system, and is lost in the capillaries. By the sudden injection of blood two distinct waves are produced, which are called the *tidal* and *percussion* waves. The tidal wave occurs whenever fluid is injected into an elastic tube (fig. 127, B), and is due to the expansion of the tube and its more gradual collapse. The percussion wave occurs (fig. 127, A) when the impulse imparted to the fluid is more sudden; this causes an abrupt upstroke of the lever, which then falls until it is again caught up perhaps by the tidal wave which begins at the same time but is not so quick.

In this way, generally speaking, the apex of the upstroke is double, the second upstroke, the so-called predicrotic elevation of the lever, representing the tidal wave. The double apex is most marked in tracings from large arteries, especially when their tone is deficient. In tracings, on the other hand, from arteries of medium size, *e.g.*, the radial, the upstroke is usually single. In this case the percussion-impulse is not sufficiently strong to jerk up the lever and produce an effect distinct from that of the systolic *wave* which immediately follows it, and

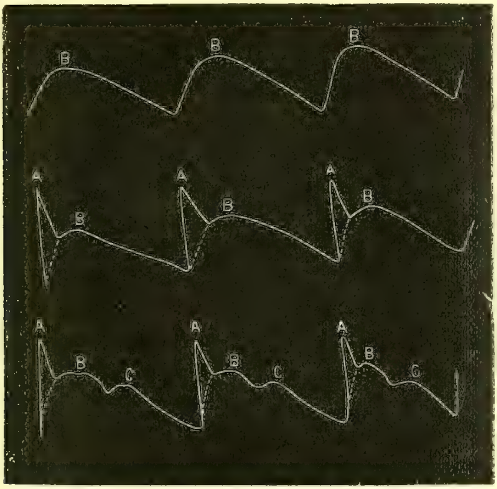

Fig. 127.—*Diagram of the formation of the pulse-tracing.* A, percussion wave; B, tidal wave; C, dicrotic wave. (Mahomed.)

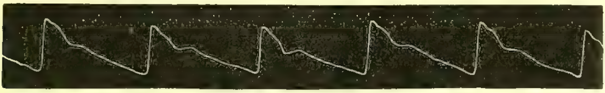

Fig. 128.—*Pulse-tracing of radial artery*, somewhat deficient in *tone*. (Sanderson.)

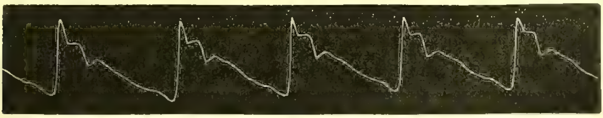

Fig. 129.—*Pulse-tracing of radial artery*, with double apex. (Sanderson.)

which continues and completes the distension. In cases of feeble arterial tension, however, the percussion-impulse may be traced by the sphygmograph, not only in the carotid pulse, but to a less extent in the radial also (fig. 129).

The interruptions in the downstroke are called the *katacrotic* waves, to distinguish them from an interruption in the upstroke, called the *anacrotic* wave, which is occasionally met with in cases in which the predicrotic or tidal wave is higher than the percussion wave.

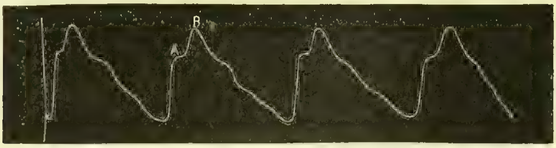

Fig. 130.—*Anacrotic pulse* from a case of aortic aneurism. A, anacrotic wave (or percussion wave). B, tidal or predicrotic wave, continued rise in tension (or higher tidal wave).

There is considerable difference of opinion as to whether the dicrotic wave is present in health generally, and also as to its cause. The balance of opinion appears to be in favour of the belief of its presence in health, although it may be very faint; while, at any rate, in certain conditions not necessarily diseased, it becomes so marked as to be quite plain to the unaided finger. Such a pulse is called *dicrotic*. Sometimes the dicrotic rise exceeds the initial upstroke, and the pulse is then called *hyper-dicrotic.*

As to the cause of dicrotism, one opinion is that it is due to a recovery of pressure during the elastic recoil, in consequence of a rebound from the periphery, and it may indeed be produced on a schema by obstructing the tube at a little distance beyond the spot where the sphygmograph is placed. Against this view, however, is the fact that the notch appears at about the same point in the downstroke in tracings from the carotid and from the radial, and not first in the radial tracing, as it should do, since that artery is nearer the periphery than the carotid, and as it does in the corresponding experiment with the arterial schema when the tube is obstructed. The generally accepted notion among clinical observers, is that the dicrotic wave is due to the rebound from the aortic valves causing a second wave; but the question cannot be considered settled, and the presence of marked dicrotism in cases of hæmorrhage, of anæmia, and of other weakening conditions, as well as its presence in cases of diminished pressure within the arteries, would imply that it might, at any rate sometimes, be due

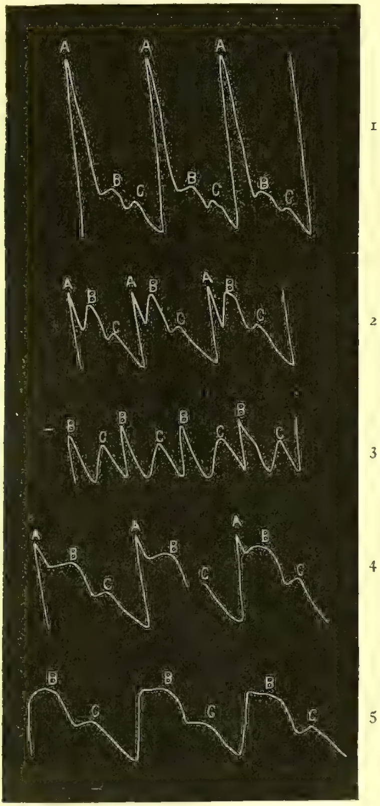

Fig. 131.—*Diagrams of pulse curves with exaggeration of one or other of the three waves.* A, percussion; B, tidal; C, dicrotic. 1, percussion wave very marked; 2, tidal wave sudden; 3, dicrotic pulse curve; 4 and 5, the tidal wave very exaggerated, from high tension. (Mahomed.)

to the altered specific gravity of the blood within the vessels, either directly or through the indirect effect of these conditions on the tone of the arterial walls. Waves may be produced in any elastic tube when a fluid is being driven through it with an intermittent force, such waves being called *waves of oscillation* (M. Foster). They have received various explanations. In an arterial schema they vary with the specific gravity of the fluid used, and with the kind of tubing, and may be therefore supposed to vary in the body with the condition of the blood and of the arteries.

Some consider the secondary waves in the downstroke of a normal wave to be due to oscillation; but, as just mentioned, even if this be the case, as is most likely, with post-dicrotic waves, the dicrotic wave itself is almost certainly due to the rebound from the aortic valves.

The anacrotic notch is usually associated with disease of the arteries, *e.g.*, in atheroma and aneurism. The dicrotic notch is called diastolic or aortic, and indicates closure of the aortic valves.

Of the three main parts then of a pulse-tracing, viz., the percussion wave, the tidal, and the dicrotic, the percussion wave is produced by sudden and forcible contraction of the heart, perhaps exaggerated by an excited action, and may be transmitted much more rapidly than the tidal wave, and so the two may be distinct; frequently, however, they are inseparable. The dicrotic wave may be as great or greater than the other two.

According to Mahomed, the distinctness of the three waves depends upon the following conditions:—

The *percussion wave* is increased by:—1. Forcible contraction of the Heart; 2. Sudden contraction of the Heart; 3. Large volume of blood; 4. Fulness of vessel; and diminished by the reversed conditions.

The *tidal wave* is increased by:—1. Slow and prolonged contraction of the Heart; 2. Large volume of blood; 3. Comparative emptiness of vessels; 4. Diminished outflow or slow capillary circulation; and diminished by the reversed conditions.

The *dicrotic wave* is increased by:—1. Sudden contraction of the Heart; 2. Comparative emptiness of vessels; 3. Increased outflow or rapid capillary circulation; 4. Elasticity of the aorta; 5. Relaxation of muscular coat; and diminished by the reversed conditions.

One very important precaution in the use of the sphygmograph lies in the careful regulation of the pressure. If the pressure be too great, the characters of the pulse may be almost entirely obscured, or the artery may be entirely obstructed, and no tracing is obtained; and on the other hand, if the pressure be too slight, a very small part of the characters may be represented on the tracing.

The Pressure of the Blood within the Arteries (producing arterial tension).

It will be understood from the foregoing that the arteries in a normal condition, are continually on the stretch during life, and in consequence of the injection of more blood at each systole of the ventricle into the elastic aorta, this stretched condition is exaggerated each time the ventricle empties itself. This condition of the arteries is due to the pressure of blood within them, because of the resistance presented by the smaller arteries and capillaries (peripheral resistance) to the emptying of the arterial system in the intervals between the contractions of the ventricle, and is called the condition of *arterial tension.* On the other hand, it must be equally clear that, as the blood is forcibly injected into the already full arteries against their elasticity, it must be subjected to the pressure of the arterial walls, the elastic recoil sending on the blood after the immediate effect of the systole has passed; so that, when an artery is cut across, the blood is projected forwards by this force for a considerable distance; at each ventricular systole, a jet of blood escaping, although the stream does not cease flowing during the diastole.

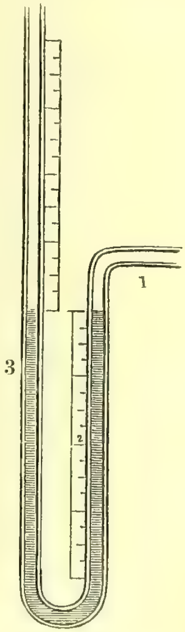

Fig. 132.—*Diagram of mercurial manometer.*

The relations which exist between the arteries and their contained blood are obviously of the utmost importance to the carrying on of the circulation, and it therefore becomes necessary to be able to gauge the alterations in blood-pressure very accurately. This may be done by means of a *mercurial manometer* in the following way:—The short horizontal limb of this (fig. 132, 1) is connected, by means of an elastic tube and cannula, with the interior of an artery; a solution of sodium or potassium carbonate being previously introduced into this part of the apparatus to prevent coagulation of the blood. The blood-pressure is thus communicated to the upper part of the mercurial column (2); and the depth to which the latter sinks, added to the height to which it rises in the other (3), will give the height of the mercurial column which the blood-pressure balances; the weight of the soda solution being subtracted.

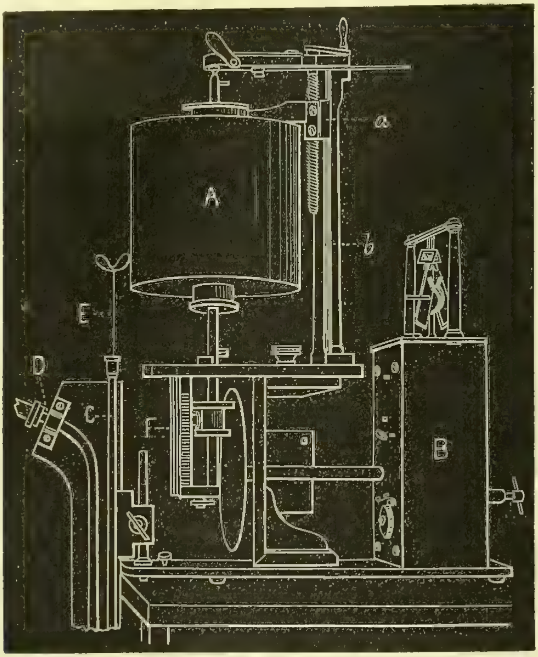

Fig. 133.—*Diagram of mercurial kymograph.* A, revolving cylinder, worked by a clockwork arrangement contained in the box (B), the speed being regulated by a fan above the box; cylinder supported by an upright (*b*), and capable of being raised or lowered by a screw (*a*), by a handle attached to it; D, C, E, represent mercurial manometer, a somewhat different form of which is shown in next figure.

For the estimation of the arterial tension at any given moment, no further apparatus than this, which is called Poiseuille's *hæmadynamometer*, is necessary; but for noting the *variations* of pressure in the arterial system, as well as its absolute amount, the instrument is usually combined with a *registering* apparatus and in this form is called a *kymograph.*

The kymograph, invented by Ludwig, is composed of a hæmadynamometer, the open mercurial column of which supports a floating piston and vertical rod, with short horizontal pen (fig. 134). The pen is adjusted in contact with a sheet of paper, which is caused to move at an uniform rate by clockwork; and thus the up-and-down movements of the mercurial column, which are communicated to the rod and pen, are marked or *registered* on the moving paper, as in the registering apparatus of the sphygmograph, and minute variations are graphically recorded (fig. 135).

For some purposes the *spring kymograph* of Fick (fig. 136) is preferable to the mercurial kymograph. It consists of a hollow C-shaped spring, filled with fluid, the interior of which is brought into connection with the interior of an artery, by means of a flexible metallic tube and cannula. In response to the pressure transmitted to its interior, the spring, *c*, tends to straighten itself, and the movement thus produced is communicated by means of a lever, *b*, to a writing-needle and registering apparatus.

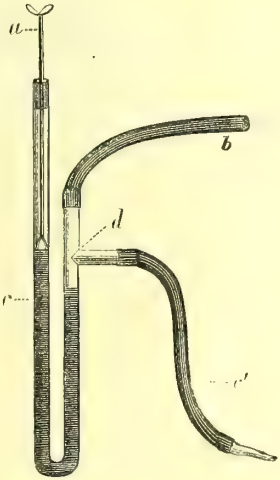

Fig. 134.—*Diagram of mercurial manometer.* *a.* Floating rod and pen. *b.* Tube, which communicates with a bottle containing an alkaline solution. *c′.* *Elastic* tube and cannula, the latter being intended for insertion in an artery.

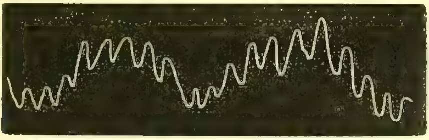

Fig. 135.—*Normal tracing of arterial pressure* in the rabbit obtained with the mercurial kymograph. The smaller undulations correspond with the heart beats; the larger curves with the respiratory movements. (Burdon-Sanderson.)

Fig. 137 exhibits an ordinary arterial pulse-tracing, as obtained by the spring-kymograph.

From observations which have been made by means of the mercurial manometer, it has been found that the pressure of blood in the carotid of a rabbit is capable of supporting a column of 2 to $3\frac{1}{2}$ inches (50 to 90 mm.), of mercury, in the dog 4 to 7 inches (100 to 175 mm.), in the horse 5 to 8 inches (150 to 200 mm.), and in man about the same.

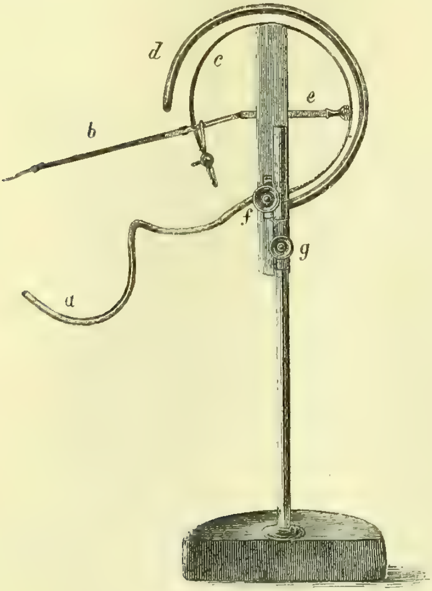

Fig. 136.—*A form of Fick's Spring Kymograph.* *a*, tube to be connected with artery; *c*, hollow spring, the movement of which moves *b*, the writing lever; *e*, screw to regulate height of *b*; *d*, outside protective spring; *g*, screw to fix on the upright of the support.

To measure the absolute amount of this pressure in any artery, it is necessary merely to multiply the area of its transverse section by the height of the column of mercury which is already known to be supported by the blood-pressure in any part of the arterial system. The weight of a column of mercury thus found will represent the pressure of the blood. Calculated in this way, the blood-pressure in the human aorta is equal to 4 lb. 4 oz. avoirdupois; that in the aorta of the horse being 11 lb. 9 oz.; and that in the radial artery at the human wrist only 4 drs. Supposing the muscular power of the right ventricle to be only one-half that of the left, the blood-pressure in the pulmonary artery will be only 2 lb. 2 oz. avoirdupois. The amounts above stated represent the arterial tension at the time of the ventricular contraction.

The blood-pressure is greatest in the left ventricle and at the beginning of the aorta, and decreases towards the capillaries. It is greatest in the arteries at the period of the ventricular systole, and is least in the auricles, during diastole, when the pressure there and in the great veins becomes, as we have seen, negative. The mean arterial pressure equals the average of the pressures in all the arteries. The pressure in the veins is never more than one-tenth of the pressure in the corresponding arteries and is greatest at the time of auricular systole. There is no periodic variation in venous pressure, as there is in the arterial, except in the great veins.

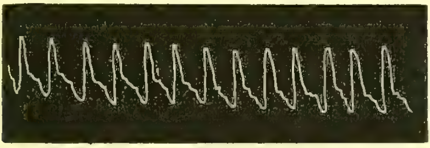

Fig. 137.—Normal arterial tracing obtained with Fick's kymograph in the dog. (Burdon-Sanderson.)

Variations of Blood-Pressure.—Many circumstances cause considerable variations in the amount of the blood-pressure. The following are the chief:—(1) *Changes in the beat of the Heart;* (2) *Changes in the Arteries and Capillaries;* (3) *Changes due to Nerve Action;* (4) *Changes in the Blood;* (5) *Respiratory Changes.*

1. *Changes in the Beat of the Heart.*—The systole and diastole of the muscular chambers. The arterial tension increases during systole and diminishes during diastole. The greater the frequency, moreover, of the heart's contractions, the greater is the blood-pressure, *cæteris paribus;* although this effect is not constant, as it may be compensated for by the delivery into the arteries at each beat of a comparatively small quantity of blood. The greater the quantity of blood expelled from the heart at each contraction the greater is the blood-pressure.

The quantity and quality of the blood nourishing the heart's substance through the coronary arteries must exercise also a very considerable influence upon its action, and therefore upon the blood-pressure.

2. *Changes in the Arteries and Capillaries.*—Variations in the degree of contraction of the smaller arteries modify the blood-

pressure by favouring or impeding the accumulation of blood in the arterial system which follows every contraction of the heart; the contraction of the arterial walls increasing the blood-pressure, while their relaxation lowers it.

3. *Changes due to Nerve Action.*—As with the heart, so with the blood-vessels the action of the nervous system is very important in relation to the blood-pressure; regulating, as it does, not only the force, frequency, and length of the heart's systole, but also the condition of the arteries, both through the central and peripheral vaso-motor centres. As this subject has not yet been fully considered it will be as well to treat of it here.

It is upon the muscular coat of the arteries that the nervous system exercises its influence; the elastic element possessing, as must be obvious, rather physical than vital properties. The muscular tissue in the walls of the vessels increases relatively to the other coats as the arteries grow smaller, so that in the smallest arteries it is developed out of all proportion to the other elements; in fact, in passing from capillary vessels, made up as we have seen of endothelial cells with a ground substance, the first change which occurs as the vessels become larger (on the side of the arteries) is the appearance of muscular fibres. Thus the nervous system is more powerful in regulating the calibre of the smaller than of the larger arteries.

It has been shown that if the cervical sympathetic nerve be divided in a rabbit, the blood-vessels of the corresponding side become dilated. The effect is best seen in the ear, which if held up to the light is seen to become redder, and the arteries to become larger. The whole ear is distinctly warmer than the opposite one. This effect is produced by removing the arteries from the influence of the central nervous system, which influence usually passes down the divided nerve; for if the peripheral end of the divided nerve (*i.e.*, that farthest from the brain) be stimulated, the arteries which were before dilated return to their natural size, and the parts regain their primitive condition. And, besides this, if the stimulus which is applied be too strong or too long continued, the point of normal constriction is passed, and the vessels become much more contracted that normal. The natural condition, which is somewhere about midway between extreme contraction and extreme dilatation, is called the natural *tone* of an artery, and if this be not maintained, the vessel is said to have lost tone, or if it be exaggerated, the tone is said to be too great. The influence of the nervous system upon the vessels consists in maintaining a natural tone. The effects described as having been produced by section of the cervical sympathetic and by subsequent stimulation are not peculiar to that nerve, as it has been found that for every part of the body there exists a nerve the division of which produces the same effects, viz., dilatation of the arteries; such may be cited as the case with the sciatic, the splanchnic nerves, and the nerves of the brachial plexus: when divided, dilatation of the blood-vessels in the parts supplied by them taking place. It appears, therefore, that nerves exist which have a distinct control over the vascular supply of a part.

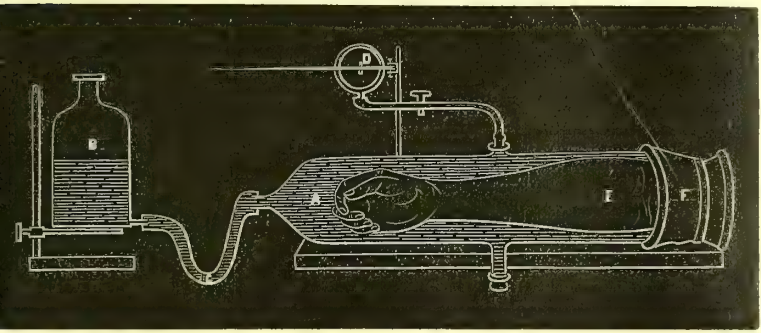

Fig. 138.—*Plethysmograph.* By means of this apparatus, the alteration in volume of the arm, E, which is enclosed in a glass tube, A, filled with fluid, the opening through which it passes being firmly closed by a thick gutta percha band, F, is communicated to the lever, D, and registered by a recording apparatus. The fluid in A communicates with that in B, the upper limit of which is above that in A. The chief alterations in volume are due to alteration in the blood contained in the arm. When the volume is increased, fluid passes out of the glass cylinder, and the lever, D, also is raised, and when a decrease takes place the fluid returns again from B to A. It will therefore be evident that the apparatus is capable of recording alterations of blood-pressure in the arm. Apparatus founded upon the same principle have been used for recording alterations in the volume of the spleen and kidney.

These nerves, are called *vaso-motor;* or, since they seem to run now in cerebro-spinal nerves, now in the sympathetic, we speak of those nerves as containing vaso-motor fibres, in addition to the fibres which have other functions.

Vaso-motor centres.—Experiments by Ludwig and others show that the vaso-motor fibres come primarily from grey matter (vaso-motor *centre*) in the interior of the medulla oblongata, between the *calamus scriptorius* and the *corpora quadrigemina.* Thence the vaso-motor fibres pass down in the interior of the spinal cord, and issuing with the anterior roots of the spinal nerves, traverse the various ganglia on the præ-vertebral cord of the sympathetic, and, accompanied by branches from these ganglia, pass to their destination.

Secondary or subordinate centres exist in the spinal cord, and local centres in various regions of the body, and through these, directly under ordinary circumstances, vaso-motor changes are also effected.

The influence exerted by the chief vaso-motor centre is called into play in several ways, but chiefly by afferent (sensory) stimuli, and it may be exerted in two ways, either to increase its usual action which maintains a medium tone of the arteries or to diminish such action. This afferent influence upon the centre may be extremely well shown by the action of a nerve the existence of which was demonstrated by Cyon and Ludwig, and which is called the *depressor,* because of its characteristic influence on the blood-pressure.

Depressor Nerve.—This small nerve arises, in the rabbit, from the superior laryngeal branch, or from this and the trunk of the pneumogastric nerve, and after communicating with filaments of the inferior cervical ganglion proceeds to the heart.

If during an observation of the blood-pressure of a rabbit this nerve be divided, and the central end (*i.e.*, that nearest the brain) be stimulated, a remarkable fall of blood-pressure ensues (fig. 139).

The cause of the fall of blood-pressure is found to proceed from the dilatation of the vascular district supplied by the splanchnic nerves, in consequence of which it holds a much larger quantity of blood than usual, and this very greatly diminishes the blood in the vessels elsewhere, and so materially affects the blood-pressure. This effect of the depressor nerve is presumed to prove that the nerve is a means of conveying to the vaso-motor centre indications of such conditions of the heart as require a diminution of the tension in the blood-vessels; as, for example, when the heart cannot, with sufficient ease, propel blood into the already too full or too tense arteries.

The action of the depressor nerve illustrates the effect of afferent impulses in causing an inhibition of the vaso-motor centre as regards its action upon certain arteries. There exist other nerves, however, the stimulation of the central end of which causes a reverse action of the centre, or, in other words, increases its tonic influence, and by causing considerable constriction of certain arterioles, either locally or generally, increases the blood-pressure. Moreover, the effect of stimulating an afferent nerve may be to dilate or constrict the arteries either generally or in the part supplied by the afferent nerve; and it is said that stimulation of an afferent nerve may produce a kind of paradoxical effect, causing *general* vascular constriction and so general increase of blood-pressure but at the same time *local* dilatation. This must evidently have an immense influence in increasing the flow of blood through a part.

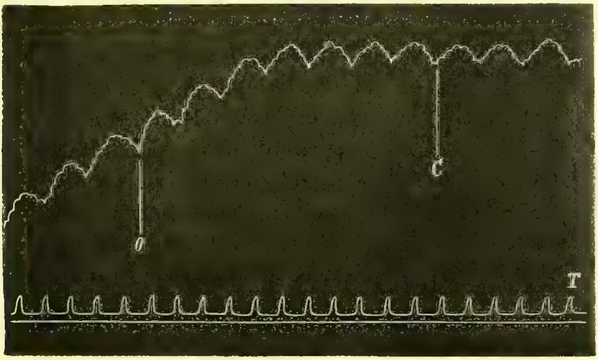

Fig. 139.—*Tracing showing the effect on blood-pressure of stimulating the central end of the Depressor nerve in the rabbit.* To be read from right to left. T, indicates the rate at which the recording-surface was travelling, the intervals correspond to seconds; C, the moment of entrance of current; O, moment at which it was shut off. The effect is some time in developing and lasts after the current has been taken off. The larger undulations are the respiratory nerves; the pulse oscillations are very small. (M. Foster.)

Not only may the vaso-motor centre be reflexly affected, but it may also be affected by impulses proceeding to it from the cerebrum, as in the case of blushing from mind disturbance, or of pallor from sudden fear. It will be shown, too, in the chapter on Respiration that the circulation of deoxygenated blood may directly stimulate the centre itself.

Local Tonic Centres.—Although the tone of the arteries is influenced by the centres in the cerebro-spinal axis, certain experiments point out that this is not the only way in which it may be affected. Thus the dilatation which occurs after section of the cervical sympathetic in the first experiment cited above, only remains for a short time, and is soon followed—although a portion of the nerve may have been removed entirely—by the vessels regaining their ordinary calibre; and afterwards local stimulation, *e.g.*, the application of heat or cold, will cause dilatation or constriction. From this it is probable that there exists a local mechanism distinct for each vascular area, and that the effect produced by the central nervous system acts through it much in the same way as the cardio-inhibitory centre in the medulla acts upon the heart through the ganglia contained within its muscular substance.

Central impulses may inhibit or increase the action of these local centres, which may be considered to be sufficient under ordinary circumstances to maintain the local tone of the vessels. The observations upon the functions of the vaso-motor nerves appear to divide them into four classes: (1) those on division of which dilatation occurs for some time, and which on stimulation of their peripheral end produce constriction; (2) those on division of which momentary dilatation followed by constriction occurs, with dilatation on stimulation; (3) those on division of which dilatation is caused, which lasts for a limited time, with constriction if stimulated at once, but dilatation if some time is allowed to elapse before the stimulation is applied: (4) a class, division of which produces no effect but which, on stimulation, cause according to their function either dilatation or constriction. A good example of this fourth class is afforded by the nerves supplying the submaxillary gland, viz., the chorda tympani and the sympathetic. When either of these nerves is simply divided, no change takes place in the vessels of the gland; but on stimulating the chorda tympani the vessels dilate, and, on the other hand, when the sympathetic is stimulated the vessels contract. The nerves acting like the chorda tympani in this case are called *vaso-dilators*, and those like the sympathetic *vaso-constrictors*. The third class, which produce at one time dilatation, at another time constriction, are believed to contain both kinds of vaso-motor nerve-fibres, or to act as dilators or contractors according to the condition of the local apparatus. It is probable that these nerves act by inhibiting or augmenting the action of the local nervous mechanism already referred to; and as they are in connection with the central nervous system, it is through this arrangement that that system is capable of influencing or of maintaining the normal local tone.

It may also be supposed that the local nerve-centres themselves may be directly affected by the condition of blood nourishing them.

The following table may serve as a summary of the effect of the nervous system upon the arteries and so upon the blood-pressure:—

A. **An increase of the blood-pressure may be produced:—**

- (1.) By stimulation of the vaso-motor centre in medulla, either
    - α. *Directly*, as by carbonated or deoxygenated blood.
    - β. *Indirectly*, by impressions descending from the cerebrum, *e.g.*, in sudden pallor.
    - γ. *Reflexly*, by stimulation of sensory nerves anywhere.
- (2.) By stimulation of the centres in spinal cord. Possibly directly or indirectly, certainly reflexly.
- (3.) By stimulation of the local centres for each vascular area, by the vaso-constrictor nerves, or directly by means of altered blood.

B. **A decrease of the blood-pressure may be produced:—**

- (1.) By stimulation of the vaso-motor centre in medulla, either
    - (α.) *Directly*, as by oxygenated or aërated blood.
    - (β.) *Indirectly*, by impressions descending from the cerebrum—*e.g.*, in blushing.
    - (γ.) *Reflexly*, by stimulation of the *depressor* nerve, and consequent dilatation of vessels of splanchnic area, and possibly by stimulation of other sensory nerves, the sensory impulse being interpreted as an indication for diminished blood-pressure.
- (2.) By stimulation of the centres in spinal cord. Possibly directly, indirectly, or reflexly.
- (3.) By stimulation of local centres for each vascular area by the vaso-dilator nerve, or directly by means of altered blood.

4. *Changes in the blood.*—*a.* As regards *quantity.* At first sight it would appear that one of the easiest ways to diminish the blood-pressure would be to remove blood from the vessels by bleeding; it has been found by experiment, however, that although the blood-pressure sinks whilst large abstractions of blood are taking place, as soon as the bleeding ceases it rises rapidly, and speedily becomes normal; that is to say, unless so large an amount of blood has been taken as to be positively

dangerous to life, abstraction of blood has little effect upon the blood-pressure. The rapid return to the normal pressure is due not so much to the withdrawal of lymph and other fluids from the body into the blood, as was formerly supposed, as to the regulation of the peripheral resistance by the vaso-motor nerves; in other words, the small arteries contract, and in so doing maintain pressure on the blood and favour its accumulation in the arterial system. This is due to the stimulation of the vaso-motor centre from diminution of the supply of blood, and therefore of oxygen. The failure of the blood-pressure to return to normal in the too great abstraction must be taken to indicate a condition of exhaustion of the centre, and consequently of want of regulation of the peripheral resistance. In the same way it might be thought that injection of blood into the already pretty full vessels would be at once followed by rise in the blood-pressure, and this is indeed the case up to a certain point—the pressure does rise, but there is a limit to the rise. Until the amount of blood injected equals about 2 to 3 per cent. of the body weight the pressure continues to rise gradually; but if the amount exceed this proportion, the rise does not continue. In this case therefore, as in the opposite when blood is abstracted, the vaso-motor apparatus must counteract the great increase of pressure by dilating the small vessels, and so diminishing the peripheral resistance, for after each rise there is a partial fall of pressure; and after the limit is reached the whole of the injected blood displaces, as it were, an equal quantity which passes into the small veins, and remains within them. It should be remembered that the veins are capable of holding the whole of the blood of the body.

The amount of blood supplied to the heart both to its substance and to its chambers, has a marked effect upon the blood-pressure.

b. As regards *quality.* The quality of the blood supplied to the heart has a distinct effect upon its contraction, as too watery or too little oxygenated blood must interfere with its action. Thus it appears that blood containing certain substances affects the peripheral resistance by acting upon the muscular fibres of the arterioles themselves or upon the local centres, and so altering directly, as it were, the calibre of the vessels.

5. *Respiratory changes* affecting the blood-pressure will be considered in the next Chapter.

Circulation in the Capillaries.

When seen in any transparent part of a living adult animal by means of the microscope (fig. 140), the blood flows with a constant equable motion; the red blood-corpuscles moving along, mostly in single file, and bending in various ways to accommodate themselves to the tortuous course of the capillary, but instantly recovering their normal outline on reaching a wider vessel.

It is in the capillaries that the chief resistance is offered to the progress of the blood; for in them the friction of the blood is greatly increased by the enormous multiplication of the surface with which it is brought in contact.

At the circumference of the stream in the larger capillaries, but chiefly in the small arteries and veins, in contact with the walls of the vessel, and adhering to them, there is a layer of liquor sanguinis which appears to be motionless. The existence of this *still layer*, as it is termed, is inferred both from the general fact that such an one exists in all fine tubes traversed by fluid, and from what can be seen in watching the movements of the blood-corpuscles. The red corpuscles occupy the middle of the stream and move with comparative rapidity; the colourless lymph-corpuscles run much more slowly by the walls of the vessel; while next to the wall there is often a transparent space in which the fluid appears to be at rest; for if any of the corpuscles happen to be forced within it, they move more slowly than before, rolling lazily along the side of the vessel, and often adhering to its wall. Part of this slow movement of the pale corpuscles and their occasional stoppage may be due to their having a natural tendency to adhere to the walls of the vessels. Sometimes, indeed, when the motion of the blood is not strong, many of the white corpuscles collect in a capillary vessel, and for a time entirely prevent the passage of the red corpuscles.

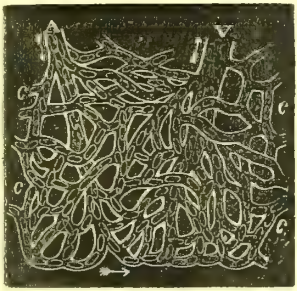

Fig. 140.—*Capillaries* (C.) *in the web of the frog's foot* connecting a small artery (A) with a small vein V (after Allen Thomson).

Intermittent flow in the Capillaries.—When the peripheral resistance is greatly diminished by the dilatation of the small arteries and capillaries, so much blood passes on from the arteries into the capillaries at each stroke of the heart, that there is not sufficient remaining in the arteries to distend them. Thus, the intermittent current of the ventricular systole is not converted into a continuous stream by the elasticity of the arteries before the capillaries are reached; and so intermittency of the flow occurs in capillaries and veins and a pulse is produced. The same phenomenon may occur when the arteries become rigid from disease, and when the beat of the heart is so slow or so feeble that the blood at each cardiac systole has time to pass on to the capillaries before the next stroke occurs, the amount of blood sent at each stroke being insufficient to properly distend the elastic arteries.

Diapedesis of Blood-Corpuscles.—Until within the last few years it has been generally supposed that the occurrence of any transudation from the interior of the capillaries into the midst of the surrounding tissues was confined, in the absence of injury, strictly to the fluid part of the blood; in other words, that the corpuscles could not escape from the circulating stream, unless the wall of the containing blood-vessel were ruptured. It is true that an English physiologist, Augustus Waller, affirmed, in 1846, that he had seen blood-corpuscles, both red and white, pass bodily through the wall of the capillary vessel in which they were contained (thus confirming what had been stated a short time previously by Addison); and that, as no opening could be seen before their escape, so none could be observed afterwards—so rapidly was the part healed. But these observations did not attract much notice until the phenomena of escape of the blood-corpuscles from the capillaries and minute veins, apart from mechanical injury, were re-discovered by Professor Cohnheim in 1867.

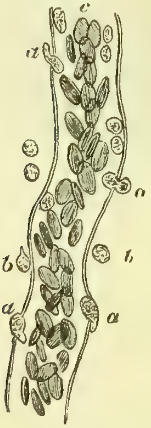

Fig. 141.—*A large capillary from the frog's mesentery* eight hours after irritation had been set up, showing emigration of leucocytes. *a*, Cells in the act of traversing the capillary wall; *b*, some already escaped. (Frey.)

Cohnheim's experiment demonstrating the passage of the corpuscles through the wall of the blood-vessel, is performed in the following manner. A frog is urarized, that is to say, paralysis is produced by injecting under the skin a minute quantity of the poison called urari; and the abdomen having been opened, a portion of small intestine is drawn out, and its transparent mesentery spread out under a microscope. After a variable time, occupied by dilatation, following contraction of the minute vessels and accompanying quickening of the blood-stream, there ensues a retardation of the current, and blood-corpuscles, both red and white, begin to make their way through the capillaries and small veins.

"Simultaneously with the retardation of the blood-stream, the leucocytes, instead of loitering here and there at the edge of the axial current, begin to crowd in numbers against the vascular wall. In this way the vein becomes lined with a continuous pavement of these bodies, which remain almost motionless, notwithstanding that the axial current sweeps by them as continuously as before, though with abated velocity. Now is the moment at which the eye must be fixed on the outer contour of the vessel, from which, here and there, minute, colourless, button-shaped elevations spring, just as if they were produced by budding out of the wall of the vessel itself. The buds increase gradually and slowly in size, until each assumes the form of a hemispherical projection, of width corresponding to that of the leucocyte. Eventually the hemisphere is converted into a pear-shaped body, the small end of which is still attached to the surface of the vein, while the round part projects freely. Gradually the little mass of protoplasm removes itself further and further away, and, as it does so, begins to shoot out delicate prongs of transparent protoplasm from its surface, in nowise differing in their aspect from the slender thread by which it is still moored to the vessel. Finally the thread is severed and the process is complete." (Burdon Sanderson.)

The process of *diapedesis* of the red corpuscles, which occurs under circumstances of impeded venous circulation, and consequently increased blood-pressure, resembles closely the migration of the leucocytes, with the exception that they are squeezed through the wall of the vessel, and do not, like them, work their way through by amæboid movement.

Various explanations of these remarkable phenomena have been suggested. Some believe that minute openings (*stigmata* or *pseudo-stomata*) between contiguous endothelial cells (p. 165) provide the means of escape for the blood-corpuscles. But the chief share in the process is to be found in the vital endowments with respect to mobility and contraction of the parts concerned—both of the corpuscles (Bastian) and the capillary wall (Stricker). Burdon-Sanderson remarks, "the capillary is not a dead conduit, but a tube of living protoplasm. There is no difficulty in understanding how the membrane may open to allow the escape of leucocytes, and close again after they have passed out ; for it is one of the most striking peculiarities of contractile substance that when two parts of the same mass are separated, and again brought into contact, they melt together as if they had not been severed."

Hitherto, the escape of the corpuscles from the interior of the blood-vessels into the surrounding tissues has been studied chiefly in connection with pathology. But it is impossible to say, at present, to what degree the discovery may not influence all present notions regarding the nutrition of the tissues, even in health.

Vital Capillary Force.—The circulation through the capillaries must, of necessity, be largely influenced by that which occurs in the vessels on either side of them—in the arteries or the veins ; their intermediate position causing them to feel at once, so to speak, any alteration in the size or rate of the arterial or venous blood-stream. Thus, the apparent contraction of the capillaries, on the application of certain irritating substances, and during fear, and their dilatation in blushing, may be referred to the action of the small arteries, rather than to that of the capillaries themselves. But largely as the capillaries are influenced by these, and by the conditions of the parts which surround and support them, their own endowments must not be disregarded. They must be looked upon, not as mere passive channels for the passage of blood, but as possessing endowments of their own (vital capillary force), in relation to the circulation. The capillary wall is actively living and contractile ; and there is no reason to doubt that, as such, it must have an important influence in connection with the blood-current.

Blood-Pressure in the Capillaries.—From observations upon the web of the frog's foot, the tongue and mesentery of the frog, the tails of newts, and small fishes (Roy and Brown), as well as upon the skin of the finger behind the nail (Kries), by careful estimation of the amount of pressure required to empty the vessels of blood under various conditions, it appears that the blood-pressure is subject to variations in the capillaries, apparently following the variations of that of the arteries; and that up to a certain point, as the extravascular pressure is increased, so does the pulse in the arterioles, capillaries, and venules become more and more evident. The pressure in the first case (web of the frog's foot) has been found to be equal to about 14 to 20 mm. of mercury; in other experiments to be equal to about $\frac{1}{5}$ to $\frac{1}{2}$ of the ordinary arterial pressure.

The Circulation in the Veins.

The blood-current in the veins is maintained by the slight vis a tergo remaining of the contraction of the left ventricle. Very effectual assistance, however, to the flow of blood is afforded by the action of the muscles capable of pressing on such veins as have valves.

The effect of such muscular pressure may be thus explained. When pressure is applied to any part of a vein, and the current of blood in it is obstructed, the portion behind the seat of pressure becomes swollen and distended as far back as to the next pair of valves. These, acting like the semilunar valves of the heart, and being, like them, inextensible both in themselves and at their margins of attachment, do not follow the vein in its distension, but are drawn out towards the axis of the canal. Then, if the pressure continues on the vein, the compressed blood, tending to move equally in all directions, presses the valves down into contact at their free edges, and they close the vein and prevent regurgitation of the blood. Thus, whatever force is exercised by the pressure of the muscles on the veins, is distributed partly in pressing the blood onwards in the proper course of the circulation, and partly in pressing it backwards and closing the valves behind (fig. 128, A and B).

The circulation might lose as much as it gains by such compression of the veins, if it were not for the numerous anastomoses by which they communicate, one with another; for through these, the closing up of the venous channel by the backward pressure is prevented from being any serious hindrance to the circulation, since the blood, of which the onward course is arrested by the closed valves, can at once pass through some anastomosing channel, and proceed on its way by another vein. Thus, therefore, the effect of muscular pressure upon veins which have valves, is turned almost entirely to the advantage of the circulation ; the pressure of the blood onwards is all advantageous, and the pressure of the blood backwards is prevented from being a hindrance by the closure of the valves and the anastomoses of the veins.

The effects of such muscular pressure are well shown by the acceleration of the stream of blood when, in venesection, the muscles of the fore-arm are put in action, and by the general acceleration of the circulation during active exercise: and the numerous movements which are continually taking place in the body while awake, though their single effects may be less striking, must be an important auxiliary to the venous circulation. Yet they are not essential ; for the venous circulation continues unimpaired in parts at rest, in paralysed limbs, and in parts in which the veins are not subject to any muscular pressure.

Rhythmical Contraction of Veins.—In the web of the bat's wing, the veins are furnished with valves, and possess the remarkable property of rhythmical contraction and dilatation, whereby the current of blood within them is distinctly accelerated. (Wharton Jones.) The contraction occurs, on an average, about ten times in a minute ; the existence of valves preventing regurgitation, the entire effect of the contractions was auxiliary to the onward current of blood. Analogous phenomena have been frequently observed in other animals.

Blood-Pressure in the Veins.—The blood-pressure gradually falls as we proceed from the heart to the arteries, from these to the capillaries, and thence along the veins to the right auricle. The blood-pressure in the veins is nowhere very great, but is greatest in the small veins, while in the large veins towards the heart the pressure becomes *negative*, or, in other words, when a vein is put in connection with a mercurial manometer the mercury will fall in the area furthest away from the vein and will rise in the area nearest the vein, having a tendency to suck in rather than to push forward. In the veins in the neck this tendency to suck in air is especially marked, and is the cause of death in some operations in that region. The amount of pressure in the brachial vein is said to support 9 mm. of mercury, whereas the pressure in the veins of the neck is about equal to a negative pressure of -3 to -8 mm.

The variations of venous pressure during systole and diastole of the heart are very slight, and a distinct pulse is seldom seen in veins except under very extraordinary circumstances.

The formidable obstacle to the upward current of the blood in the veins of the trunk and extremities in the erect posture supposed to be presented by the gravitation of the blood, has no real existence, since the pressure exercised by the column of blood in the arteries, will be always sufficient to support a column of venous blood of the same height as itself: the two columns mutually balancing each other. Indeed, so long as both arteries and veins contain continuous columns of blood, the force of gravitation, whatever be the position of the body, can have no power to move or resist the motion of any part of the blood in any direction. The lowest blood-vessels have, of course, to bear the greatest amount of pressure; the pressure on each part being directly proportionate to the height of the column of blood above it: hence their liability to distension. But this pressure bears equally on both arteries and veins, and cannot either move, or resist the motion of, the fluid they contain, so long as the columns of fluid are of equal height in both, and continuous.

Velocity of the Circulation.

The velocity of the blood-current at any given point in the various divisions of the circulatory system is inversely proportional to their sectional area at that point. If the sectional area of all the branches of a vessel united were always the same as that of the vessel from which they arise, and if the aggregate sectional area of the capillary vessels were equal to that of the aorta, the mean rapidity of the blood's motion in the capillaries would be the same as in the aorta and largest arteries; and if a similar correspondence of capacity existed in the veins and arteries, there would be an equal correspondence in the rapidity of the circulation in them. But the arterial and venous systems may be represented by two truncated cones with their apices directed towards the heart; the area of their united base (the sectional area of the capillaries) being 400—800 times as great as that of the truncated apex representing the aorta. Thus the velocity of blood in the capillaries is at least $\frac{1}{400}$ of that in the aorta.

Velocity in the Arteries.—The velocity of the stream of blood is greater in the arteries than in any other part of the circulatory system, and in them it is greatest in the neighbourhood of the heart, and during the ventricular systole; the rate of movement diminishing during the diastole of the ventricles, and in the parts of the arterial system most distant from the heart. Chauveau has estimated the rapidity of the blood-stream in the carotid of the horse at over 20 inches per second during the heart's systole, and nearly 6 inches during the diastole (520—150 mm.).

Estimation of the Velocity.—Various instruments have been devised for measuring the velocity of the blood-stream in the arteries. Ludwig's "*Stromuhr*" (fig. 142) consists of an U-shaped glass tube dilated at *a* and *a*′, and whose extremities, *h* and *i*, are of known calibre. The bulbs can be filled by a common opening at *k*. The instrument is so contrived that at *b* and *b*′ the glass part is firmly fixed into metal cylinders, which are fixed into a circular horizontal table, *c c*′, capable of horizontal movement on a similar table *d d*′ about the vertical axis marked in figure by a dotted line. The opening in *c c*′, when the instrument is in position, as in fig., corresponds exactly with those in *d d*′; but if *c c*′ be turned at right angles to its present position, there is no communication between *h* and *a*, and *i* and *a*′, but *h* communicates directly with *i*; and if turned through two right angles *c*′ communicates with *d*, and *c* with *d*′, and there is no direct connection between *h* and *i*. The experiment is performed in the following way:—The artery to be experimented upon is divided and connected with two cannulæ and tubes which fit it accurately with *h* and *i*—*h* the central end,

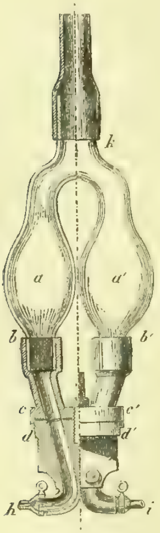

Fig. 142.—*Ludwig's Stromuhr.*

and *i* the peripheral; the bulb *a* is filled with olive oil up to a point rather lower than *k*, and *a′* and the remainder of *a* is filled with defibrinated blood; the tube on *k* is then carefully clamped; the tubes *d* and *d′* are also filled with defibrinated blood. When everything is ready, the blood is allowed to flow into *a* through *h*, and it pushes before it the oil, and that the defibrinated blood into the artery through *i*, and replaces it in *a′*; when the blood reaches the former level of the oil in *a*, the disc *c c′* is turned rapidly through two right angles, and the blood flowing through *d* into *a′* again displaces the oil which is driven into *a*. This is repeated several times, and the duration of the experiment noted. The capacity of *a* and *a′* is known; the diameter of the artery is also known by its corresponding with the cannulæ of known diameter, and as the number of times *a* has been filled in a given time is known, the velocity of the current can be calculated.

Chauveau's instrument (fig. 143) consists of a thin brass tube, *a*, in one side of which is a small perforation closed by thin vulcanised indiarubber. Passing through the rubber is a fine lever, one end of which, slightly flattened, extends into the *lumen* of the tube, while the other moves over the face of a dial. The tube is inserted into the interior of an artery, and ligatures applied to fix it, so that the movement of the blood may, in flowing through the tube, be indicated by the movement of the outer extremity of the lever on the face of the dial.

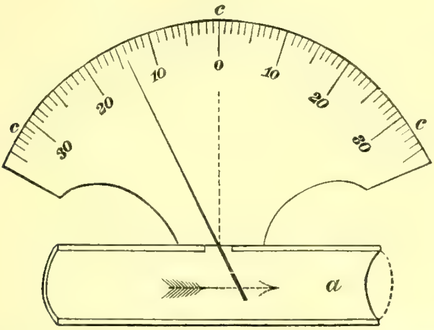

Fig. 143.—*Diagram of Chauveau's Instrument.* *a.* Brass tube for introduction into the lumen of the artery, and containing an index-needle, which passes through the elastic membrane in its side, and moves by the impulse of the blood-current. *c.* Graduated scale, for measuring the extent of the oscillations of the needle.

The *Hæmatochometer* of Vierordt, and the instrument of Lortet, resemble in principle that of Chauveau.

Velocity in the Capillaries.—The observations of Hales, E. H. Weber, and Valentin agree very closely as to the rate of the blood-current in the capillaries of the frog; and the mean of their estimates gives the velocity of the *systemic* capillary circulation at about one inch (25 mm.) per minute. The velocity in the capillaries of warm-blooded animals is greater. In the dog $\frac{1}{50}$ to $\frac{3}{100}$ inch (·5 to ·75 mm.) a second. This may seem inconsistent with the facts which show that the whole circulation is accomplished in about half a minute. But the whole length of capillary vessels, through which any given portion of blood has to pass, probably does not exceed from $\frac{1}{30}$th to $\frac{1}{50}$th of an inch (.5 mm.); and therefore the time required for each quantity of blood to traverse its own appointed portion of the general capillary system will scarcely amount to a second.

Velocity in the Veins.—The *velocity* of the blood is greater in the veins than in the capillaries, but less than in the arteries: this fact depending upon the relative capacities of the arterial and venous systems. If an accurate estimate of the proportionate areas of arteries and the veins corresponding to them could be made, we might, from the velocity of the arterial current, calculate that of the venous. An usual estimate is, that the capacity of the veins is about twice or three times as great as that of the arteries, and that the velocity of the blood's motion is, therefore, about twice or three times as great in the arteries as in the veins, 8 inches (about 200 mm.) a second. The rate at which the blood moves in the veins gradually increases the nearer it approaches the heart, for the sectional area of the venous trunks, compared with that of the branches opening into them, becomes gradually less as the trunks advance towards the heart.

Velocity of the Circulation as a whole.—It would appear that a portion of blood can traverse the entire course of the circulation, in the horse, in half a minute. Of course it would require longer to traverse the vessels of the most distant part of the extremities than to go through those of the neck: but taking an average length of vessels to be traversed, and assuming, as we may, that the movement of blood in the human subject is not slower than in the horse, it may be concluded that half a minute represents the average rate.

Satisfactory data for these estimates are afforded by the results of experiments to ascertain the rapidity with which poisons introduced into the blood are transmitted from one part of the vascular system to another. The time required for the passage of a solution of potassium ferrocyanide, mixed with the blood, from one jugular vein (through the right side of the heart, the pulmonary vessels, the left cavities of the heart, and the general circulation) to the jugular vein of the opposite side, varies from twenty to thirty seconds. The same substance was transmitted from the jugular vein to the great saphena in twenty seconds; from the jugular vein to the masseteric artery, in between fifteen and thirty seconds; to the facial artery, in one experiment, in between ten and fifteen seconds; in another experiment in between twenty and twenty-five seconds; in its transit from the jugular vein to the metatarsal artery, it occupied between twenty and thirty seconds, and in one instance more than forty seconds. The result was nearly the same whatever was the rate of the heart's action.

In all these experiments, it is assumed that the substance injected moves with the blood, and at the same rate, and does not move from one part of the organs of circulation to another by diffusing itself through the blood or tissues more quickly than the blood moves. The assumption is sufficiently probable, to be considered nearly certain, that the times above mentioned, as occupied in the passage of the injected substances, are those in which the portion of blood, into which each was injected, was carried from one part to another of the vascular system.

Another mode of estimating the general velocity of the circulating blood, is by calculating it from the quantity of blood supposed to be contained in the body, and from the quantity which can pass through the heart in each of its actions. But the conclusions arrived at by this method are less satisfactory. For the estimates both of the total quantity of blood, and of the capacity of the cavities of the heart, have as yet only approximated to the truth. Still the most careful of the estimates thus made accord very nearly with those already mentioned; and it may be assumed that the blood may all pass through the heart in from twenty-five to fifty seconds.

Peculiarities of the Circulation in Different Parts.—The most remarkable peculiarities attending the circulation of blood through different organs are observed in the cases of the *brain*, the *erectile organs*, the *lungs*, the *liver*, and the *kidney*.

1. *In the Brain.*—For the due performance of its functions, the brain requires a large supply of blood. This object is effected through the number and size of its arteries, the two *internal carotids*, and the two *vertebrals*. It is further necessary that the force with which this blood is sent to the brain should be less, or at least should be subject to less variation from external circumstances than it is in other parts, and so the large arteries are very tortuous and anastomose freely in the circle of Willis, which thus insures that the supply of blood to the brain is uniform, though it may by an accident be diminished, or in some way changed, through one or more of the principal arteries. The transit of the large arteries through bone, especially the carotid canal of the temporal bone, may prevent any undue distension; and uniformity of supply is further insured by the arrangement of the vessels in the pia mater, in which, previous to their distribution to the substance of the brain, the large arteries break up and divide into innumerable minute branches ending in capillaries, which, after frequent communications with one another, enter the brain, and carry into nearly every part of it uniform and equable streams of blood. The arteries are also enveloped in a special lymphatic sheath. The arrangement of the *veins* within the cranium is also peculiar. The large venous trunks or sinuses are formed so as to be scarcely capable of change of size; and composed, as they are, of the tough tissue of the dura mater, and, in some instances, bounded on one side by the bony cranium, they are not compressible by any force which the fulness of the arteries might exercise through the substance of the brain; nor do they admit of distension when the flow of venous blood from the brain is obstructed.

The general uniformity in the supply of blood to the brain, which is thus secured, is well adapted, not only to its functions, but also to its condition as a mass of nearly incompressible substance placed in a cavity with unyielding walls. These conditions of the brain and skull have appeared, indeed, to some, enough to justify the opinion that the quantity of blood in the brain must be at all times the same. It was found that in animals bled to death, without any aperture being made in the cranium, the brain became pale and anæmic like other parts. And in death from strangling or drowning, congestion of the cerebral vessels; while in death by prussic acid, the quantity of blood in the cavity of the cranium was determined by the position in which the animal was placed after death, the cerebral vessels being congested when the animal was suspended with its head downwards, and comparatively empty when the animal was kept suspended by the ears. That, it was concluded, although the total volume of the contents of the cranium is probably nearly always the same, yet the quantity of blood in it is liable to variation, its increase or diminution being accompanied by a simultaneous diminution or increase in the quantity of the cerebro-spinal fluid, which, by readily admitting of being removed from one part of the brain and spinal cord to another, and of being rapidly absorbed, and as readily effused, would serve as a kind of supplemental fluid to the other contents of the cranium, to keep it uniformly filled in case of variations in their quantity (Burrows). And there can be no doubt that, although the arrangements of the blood-vessels, to which reference has been made, ensure to the brain an amount of blood which is tolerably uniform, yet, inasmuch as with every beat of the heart and every act of respiration, and under many other circumstances, the quantity of blood in the cavity of the cranium is constantly varying, it is plain that, were there not provision made for the possible displacement of some of the contents of the unyielding bony case in which the brain is contained, there would be often alternations of excessive pressure with insufficient supply of blood. Hence we may consider that the cerebro-spinal fluid in the interior of the skull not only subserves the mechanical functions of fat in other parts as a *packing* material, but by the readiness with which it can be displaced into the spinal canal, provides the means whereby undue pressure and insufficient supply of blood are equally prevented.

Chemical Composition of Cerebro-spinal Fluid.—The cerebro-spinal fluid is transparent, colourless, not viscid, with a saline taste and alkaline reaction, and is not affected by heat or acids. It contains 981—984 parts water, sodium chloride, traces of potassium chloride, of sulphates, carbonates, alkaline and earthy phosphates, minute traces of urea, sugar, sodium lactate, fatty matter, cholesterin, and albumen (Flint).

2. *In Erectile Structures.*—The instances of greatest variation in the quantity of blood contained, at different times, in the same organs, are found in certain structures which, under ordinary circumstances, are soft and flaccid, but, at certain times, receive an unusually large quantity of blood, become distended and swollen by it, and pass into the state which has been termed *erection.* Such structures are the *corpora cavernosa* and *corpus spongiosum* of the penis in the male, and the *clitoris* in the female; and, to a less degree, the *nipple* of the mammary gland in both sexes. The corpus cavernosum penis, which is the best example of an erectile structure, has an external fibrous membrane or sheath; and from the inner surface of the latter are prolonged numerous fine lamellæ which divide its cavity into small compartments looking like cells when they are inflated. Within these is situated the plexus of veins upon which the peculiar erectile property of the organ mainly depends. It consists of short veins which very closely interlace and anastomose with each other in all directions, and admit of great variation of size, collapsing in the passive state of the organ, but, for erection, capable of an amount of dilatation which exceeds beyond comparison that of the arteries and veins which convey the blood to and from them. The strong fibrous tissue lying in the intervals of the venous plexuses, and the external fibrous membrane or sheath with which it is connected, limit the distension of the vessels, and, during the state of erection, give to the penis its condition of tension and firmness. The same general condition of vessels exists in the corpus spongiosum urethræ, but around the urethra the fibrous tissue is much weaker than around the body of the penis, and around the glans there is none. The venous blood is returned from the plexuses by comparatively small veins; those from the glans and the fore part of the urethra empty themselves into the dorsal veins of the penis; those from the cavernosum pass into deeper veins which issue from the corpora cavernosa at the crura penis; and those from the rest of the urethra and bulb pass more directly into the plexus of the veins about the prostate. For all these veins one condition is the same; namely, that they are

liable to the pressure of muscles when they leave the penis. The muscles chiefly concerned in this action are the erector penis and accelerator urinæ. Erection results from the distension of the venous plexuses with blood. The principal exciting cause in the erection of the penis is nervous irritation, originating in the part itself, or derived from the brain and spinal cord. The nervous influence is communicated to the penis by the pudic nerves, which ramify in its vascular tissue: and after their division in the horse, the penis is no longer capable of erection.

This influx of the blood is the first condition necessary for erection, and through it alone much enlargement and turgescence of the penis may ensue. But the erection is probably not complete, nor maintained for any time except when, together with this influx, the muscles already mentioned contract, and by compressing the veins, stop the efflux of blood, or prevent it from being as great as the influx.

It appears to be only the most perfect kind of erection that needs the help of muscles to compress the veins; and none such can materially assist the erection of the nipples, or that amount of turgescence, just falling short of erection, of which the spleen and many other parts are capable. For such turgescence nothing more seems necessary than a large plexiform arrangement of the veins, and such arteries as may admit, upon occasion, augmented quantities of blood.

(3, 4, 5). *The circulation in the Lungs, Liver, and Kidneys* will be described under those heads.

Agents concerned in the circulation.—Before quitting this subject it will be as well to bring together in a tabular form the various agencies concerned in maintaining the circulation.

1. The *Systole and Diastole of the Heart*, the former pumping into the aorta and so into the arterial system a certain amount of blood, and the latter to some extent sucking in the blood from the veins.

2. *The elastic and muscular coats of the arteries*, which serve to keep up an equable and continuous stream.

3. The so-called *vital capillary force.*

4. The pressure of the *muscles on veins with valves*, and the slight rhythmic contraction of the veins.

5. *Aspiration of the thorax* during inspiration, by means of which

the blood is drawn from the large veins into the thorax (to be treated of in next Chapter).

Discovery of the Circulation.

Up to nearly the close of the sixteenth century it was generally believed that the blood passed from one ventricle to the other through foramina in the "septum ventriculorum." These foramina are of course purely imaginary, but no one ventured to dispute their existence till Servetus boldly stated that he could not succeed in finding them. He further asserted that the blood passed from the Right to the Left side of the heart by way of the lungs, and also advanced the hypothesis that it is thus "revivified," remarking that the Pulmonary Artery is too large to serve merely for the nutrition of the lungs (a theory then generally accepted).

Realdus, Columbo, and Cæsalpinus added several important observations. The latter showed that the blood is slightly cooled by passing through the lungs. also that the veins swell up on the distal side of a ligature. The existence of valves in the veins had previously been discovered by Fabricius of Aquapendente, the teacher of Harvey.

The honour of first demonstrating the general course of the circulation belongs by right to Harvey, who made his grand discovery about 1618. He was the first to establish the muscular structure of the heart, which had been denied by many of his predecessors; and by careful study of its action both in the body and when excised, ascertained the order of contraction of its cavities. He did not content himself with inferences from the anatomy of the parts, but employed the experimental method of injection, and made an extensive and accurate series of observations on the circulation in cold-blooded animals. He forced water through the Pulmonary Artery till it trickled out through the Left Ventricle, the tip of which had been cut off. Another of his experiments was to fill the Right side of the heart with water, tie the Pulmonary Artery and the Venæ Cavæ and then squeeze the Right ventricle: not a drop could be forced through into the Left ventricle, and thus he conclusively disproved the existence of foramina in the septum ventriculorum. "I have sufficiently proved," says he, "that by the beating of the heart the blood passes from the veins into the arteries through the ventricles, and is distributed over the whole body."

"In the warmer animals, such as man, the blood passes from the Right Ventricle of the Heart through the Pulmonary Artery into the Lungs, and thence through the Pulmonary Veins into the Left Auricle, thence into the Left Ventricle."

Proofs of the Circulation of the Blood.—The following are the main arguments by which Harvey established the fact of the circulation:—

1. The heart in half an hour propels more blood than the whole mass of blood in the body.

2. The great force and jetting manner with which the blood spurts from an opened artery, such as the carotid, with every beat of the heart.

3. If true, the normal course of the circulation explains why after death the arteries are commonly found empty and the veins full.

4. If the large *veins* near the heart were tied in a fish or snake, the heart became pale, flaccid, and bloodless; on removing the ligature, the blood again flowed into the heart. If the *artery* were tied, the heart became distended; the distension lasting until the ligature was removed.

5. The evidence to be derived from a ligature round a limb. If it be drawn very tight, no blood can enter the limb, and it becomes pale and cold. If the ligature be somewhat relaxed, blood can enter but cannot leave the limb; hence it becomes swollen and congested. If the ligature be removed, the limb soon regains its natural appearance.

6. The existence of valves in the veins which only permit the blood to flow towards the heart.

7. The general constitutional disturbance resulting from the introduction of a poison at a single point, *e. g.*, snake poison.

To these may now be added many further proofs which have accumulated since the time of Harvey, *e. g.* :—

8. Wounds of arteries and veins. In the former case hæmorrhage may be almost stopped by pressure between the heart and the wound, in the latter by pressure beyond the seat of injury.

9. The direct observation of the passage of blood corpuscles from small arteries through capillaries into veins in all transparent vascular parts, as the mesentery, tongue or web of the frog, the tail or gills of a tadpole, &c.

10. The results of injecting certain substances into the blood.

Further, it is obvious that the mere fact of the existence of a hollow muscular organ (the heart) with valves so arranged as to permit the blood to pass only in one direction, of itself suggests the course of the circulation. The only part of the circulation which Harvey could not follow is that through the capillaries, for the simple reason that he had no lenses sufficiently powerful to enable him to see it. Malpighi (1661) and Leeuwenhoek (1668) demonstrated it in the tail of the tadpole and lung of the frog.

CHAPTER VI.

RESPIRATION.

THE maintenance of animal life necessitates the continual absorption of oxygen and excretion of carbonic acid; the blood being, in all animals which possess a well developed blood-vascular system, the medium by which these gases are carried. By the blood, oxygen is absorbed from without and conveyed to all parts of the organism; and, by the blood, carbonic acid, which comes from within, is carried to those parts by which it may escape from the body. The two processes,—absorption of oxygen and excretion of carbonic acid,—are complementary, and their sum is termed the process of *Respiration.*

In all Vertebrata, and in a large number of Invertebrata, certain parts, either *lungs or gills,* are specially constructed for bringing the blood into proximity with the aërating medium (atmospheric air, or water containing air in solution). In some of the lower Vertebrata (frogs and other naked Amphibia) the skin is important as a respiratory organ, and is capable of supplementing, to some extent, the functions of the *proper breathing* apparatus; but in all the higher animals, including man, the respiratory capacity of the skin is so infinitesimal that it may be practically disregarded.

Essentially, a lung or gill is constructed of a fine transparent membrane, one surface of which is exposed to the air or water, as the case may be, while, on the other, is a network of blood-vessels,—the only separation between the blood and aërating medium being the thin wall of the blood-vessels, and the fine membrane on one side of which vessels are distributed. The difference between the simplest and the most complicated respiratory membrane is one of degree only.

The various complexity of the respiratory membrane, and the kind of aërating medium, are not, however, the only conditions which cause a difference in the respiratory capacity of different animals. The number and size of the red blood-corpuscles, the mechanism of the breathing apparatus, the presence or absence of a *pulmonary* heart, physiologically distinct from the *systemic*, are, all of them, conditions scarcely second in importance.

In the heart of man and all other Mammalia, the *right* side from which the blood is propelled into and through the lungs may be termed the "pulmonary" heart; while the *left* side is "systemic" in function. In many of the lower animals, however, no such distinction can be drawn. Thus, in Fish the heart propels the blood to the respiratory organs (gills); but there is no contractile sac corresponding to the left side of the heart, to propel the blood directly into the systemic vessels.

It may be well to state here that the lungs are only the medium for the *exchange*, on the part of the blood, of carbonic acid for oxygen. They are not the seat, in any special manner, of those combustion-processes of which the production of carbonic acid is the final result. These occur in all parts of the body—more in one part, less in another: chiefly in the substance of the tissues, but in part in the capillary blood-vessels contained in them.

The Respiratory Passages and Tissues.

The object of respiration is the interchange of gases in the lungs; for this purpose it is necessary that the atmospheric air shall pass into them and be expelled from them. The lungs are contained in the *chest* or *thorax*, which is a closed cavity having no communication with the outside, except by means of the respiratory passages. The air enters these passages through the nostrils or through the mouth, thence it passes through the *larynx* into the *trachea* or windpipe, which about the middle of the chest divides into two tubes, *bronchi*, one to each (right and left) lung.

The Larynx is the upper part of the passage which leads exclusively to the lung; it is formed by the thyroid, cricoid, and arytenoid cartilages (fig. 145), and contains the *vocal cords*, by the vibration of which the voice is chiefly produced. These vocal cords are ligamentous bands attached to certain cartilages capable of movement by muscles. By their approximation the cords can entirely close the entrance into the larynx; but under the ordinary conditions, the entrance of the larynx is formed by a more or less triangular chink between them, called the *rima glottidis*. Projecting at an acute angle between the base of the tongue and the larynx to which it is attached, is a leaf-shaped cartilage, with its larger extremity free, called the *epiglottis* (fig. 145, *e*). The whole of the larynx is lined by mucous membrane, which, however, is extremely thin over the cords. At its lower extremity the larynx joins the trachea.* With the exception of the epiglottis and the so-called cornicula laryngis, the cartilages of the larynx are of the *hyaline* variety.

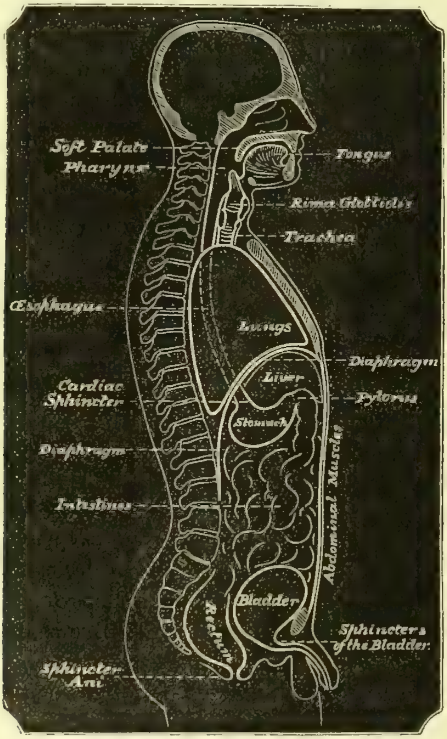

Fig. 144.

Structure of Epiglottis.—The supporting cartilage is composed of yellow elastic cartilage, enclosed in a fibrous sheath (perichondrium), and covered on both sides with mucous membrane.

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* A detailed account of the structure and function of the Larynx will be found in Chapter XVI.

The *anterior* surface, which looks towards the base of the tongue, is covered with mucous membrane, the basis of which is fibrous tissue, elevated towards both surfaces in the form of rudimentary papillæ, and covered with several layers of squamous epithelium. In it ramify capillary blood-vessels, and in its meshes are a large number of lymphatic channels. Under the mucous membrane, in the less dense fibrous tissue of which it is composed, are a number of tubular glands. The *posterior* or laryngeal surface of the epiglottis is covered by a mucous membrane, similar in structure to that on the other surface, but that the epithelial coat is thinner, the number of strata of cells being less, and the papillæ few and less distinct. The fibrous tissue which constitutes the mucous membrane is in great part of the adenoid variety, and this is here and there collected into distinct masses or follicles. The glands of the posterior surface are smaller but more numerous than those on the other surface. In many places the glands which are situated nearest to the perichondrium are directly continuous through apertures in the cartilage with those on the

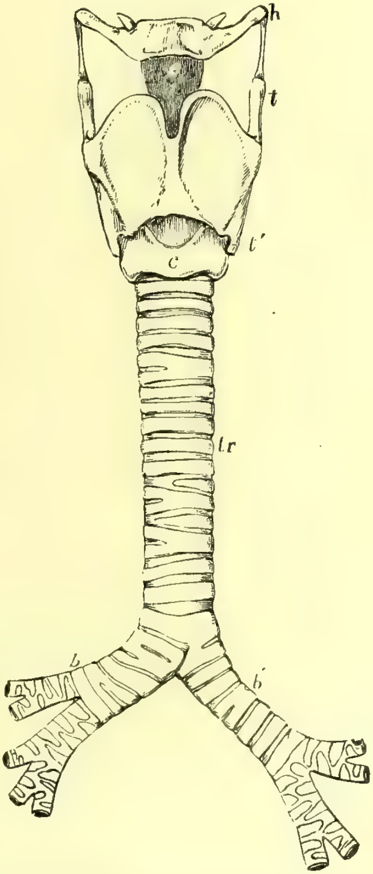

Fig. 145.—*Outline showing the general form of the larynx, trachea, and bronchi, as seen from before.* *h*, the great cornu of the hyoid bone; *e*, epiglottis; *t*, superior, and *t′*, inferior cornu of the thyroid cartilage; *c*, middle of the cricoid cartilage; *tr*, the trachea, showing sixteen cartilaginous rings; *b*, the right, and *b′*, the left bronchus. (Allen Thomson.) × ½.

other side, and often the ducts of the glands from one side of the cartilage pass through and open on the mucous surface of the other side. *Taste goblets* have been found in the epithelium of the posterior surface of the epiglottis, and in several other situations in the laryngeal mucous membrane.

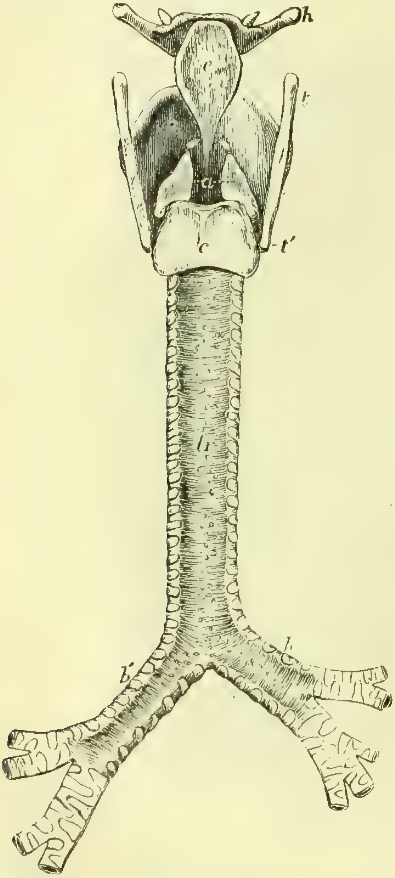

Fig. 146.—*Outline showing the general form of the larynx, trachea, and bronchi as seen from behind.* *h*, great cornu of the hyoid bone; *t*, superior, and *t′*, the inferior cornu of the thyroid cartilage; *e*, the epiglottis; *a*, points to the back of both the arytenoid cartilages, which are surmounted by the cornicula; *c*, the middle ridge on the back of the cricoid cartilage; *tr*, the posterior membranous part of the trachea; *b*, *b′*, right and left bronchi. (Allen Thomson.) ½.

The Trachea and Bronchial Tubes.—The *trachea* or wind-pipe extends from the cricoid cartilage, which is on a level with the fifth cervical vertebra, to a point opposite the third dorsal vertebra, where it divides into the two bronchi, one for each lung (fig. 146). It measures, on an average, four or four-and-a-half inches in length, and from three-quarters of an inch to an inch in diameter.

Structure.—The trachea is essentially a tube of fibro-elastic membrane, within the layers of which are enclosed a series of cartilaginous rings, from sixteen to twenty in number. These rings extend only around the front and sides of the trachea (about two-thirds of its circumference), and are deficient behind; the interval between their posterior extremities being bridged over by a continuation of the fibrous membrane in which they are enclosed (fig. 145). The cartilages of the trachea and bronchial tubes are of the *hyaline* variety.

Immediately within this tube, at the back, is a layer of unstriped muscular fibres, which extends, *transversely*, between the ends of the cartilaginous rings to which they are attached, and opposite the intervals between them, also ; their evident function being to diminish, when required, the calibre of the trachea by approximating the ends of the cartilages. Outside these are a few *longitudinal* bundles of muscular tissue, which, like the preceding, are attached both to the fibrous and cartilaginous framework.

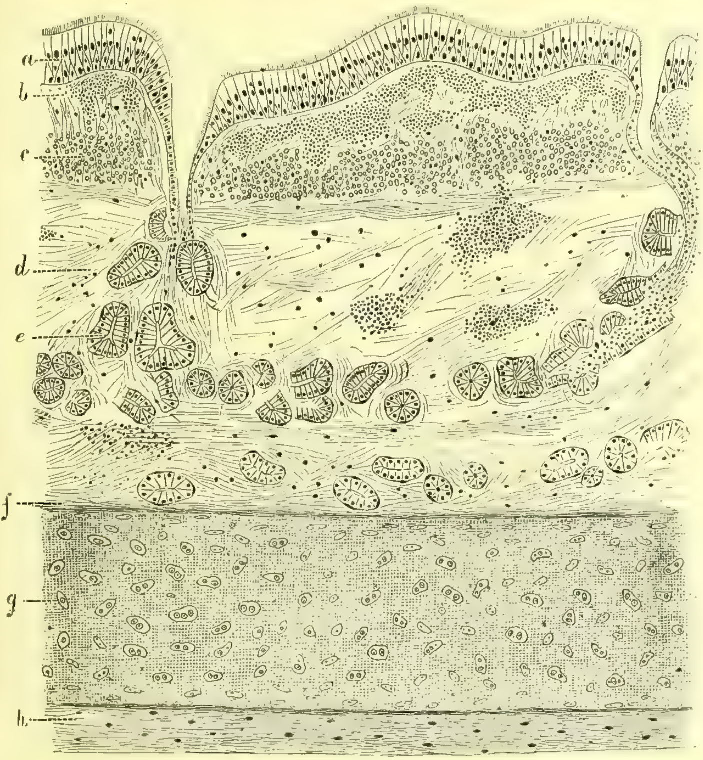

Fig. 147.—*Section of trachea.* *a*, columnar ciliated epithelium ; *b* and *c*, proper structure of the mucous membrane, containing elastic fibres cut across transversely ; *d*, submucous tissue containing mucous glands, *e*, separated from the hyaline cartilage, *g*, by a fine fibrous tissue, *f* ; *h*, external investment of fine fibrous tissue. (S. K. Alcock.)

The mucous membrane consists of adenoid tissue, separated from the stratified columnar epithelium which lines it by a homogeneous basement membrane. This is penetrated here and there by channels which connect the adenoid tissue of the *mucosa* with the intercellular substance of the epithelium. The stratified columnar epithelium is formed of several layers of cells (fig. 147), of which the most superficial layer is ciliated, and is often branched downwards to join connective-tissue corpuscles; while between these branched cells are smaller elongated cells prolonged up towards the surface and down to the basement membrane. Beneath these are one or more layers of more irregularly shaped cells. In the deeper part of the mucosa are many elastic fibres between which lie connective-tissue corpuscles and capillary blood-vessels.

Numerous mucous glands are situate on the exterior and in the substance of the fibrous framework of the trachea; their ducts perforating the various structures which form the wall of the trachea, and opening through the mucous membrane into the interior.

The two bronchi into which the trachea divides, of which the right is shorter, broader, and more horizontal than the left (fig. 145), resemble the trachea exactly in structure, and in the arrangement of their cartilaginous rings. On entering the substance of the lungs, however, the rings, although they still form only larger or smaller segments of a circle, are no longer confined to the front and sides of the tubes, but are distributed impartially to all parts of their circumference.

The bronchi divide and sub-divide, in the substance of the lungs, into a number of smaller and smaller branches, which penetrate into every part of the organ, until at length they end in the smaller sub-divisions of the lungs, called *lobules.*

All the larger branches still have walls formed of tough membrane, containing portions of cartilaginous rings, by which they are held open, and unstriped muscular fibres, as well as longitudinal bundles of elastic tissue. They are lined by mucous membrane, the surface of which, like that of the larynx and trachea, is covered with ciliated epithelium (fig. 148). The mucous membrane is abundantly provided with mucous glands.

As the bronchi become smaller and smaller, and their walls thinner, the cartilaginous rings become scarcer and more irregular, until, in the smaller bronchial tubes, they are represented only by minute and scattered cartilaginous flakes. And when the bronchi, by successive branches are reduced to about $\frac{1}{40}$ of an inch in diameter, they lose their cartilaginous element altogether, and their walls are formed only of a tough fibrous elastic membrane, with circular muscular fibres ; they are still lined, however, by a thin mucous membrane, with ciliated epithelium, the length of the cells bearing the cilia having become so far diminished, that the cells are now almost cubical. In the smaller bronchi the circular muscular fibres are more abundant than in the trachea and larger bronchi, and form a distinct circular coat.

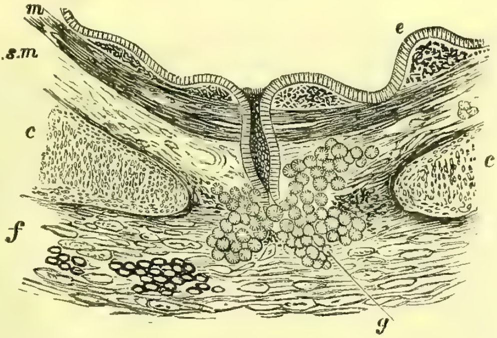

Fig. 148.—*Transverse section of a bronchus*, about ¼ inch in diameter. *e*, Epithelium (ciliated) ; immediately beneath it is the mucous membrane or internal fibrous layer, of varying thickness ; *m*, muscular layer ; *s, m*, submucous tissue ; *f*, fibrous tissue ; *c*, cartilage enclosed within the layers of fibrous tissue ; *g*, mucous gland. (F. E. Schulze.)

The Lungs and Pleura.—The Lungs occupy the greater portion of the thorax. They are of a spongy elastic texture, and on section appear to the naked eye as if they were in great part solid organs, except here and there, at certain points, where branches of the bronchi or air-tubes may have been cut across, and show, on the surface of the section, their tubular structure. In fact, however, the lungs are hollow organs, each of which communicates by a separate orifice with a common air-tube, the *trachea.*

The Pleura.—Each lung is enveloped by a serous membrane—the *pleura*, one layer of which adheres closely to the surface of the lung, and provides it with its smooth and slippery covering, while the other adheres to the inner surface of the chest-wall. The continuity of the two layers, which form a closed sac, as in the case of other serous membranes, will be best understood by reference to fig. 149. The appearance of a space, however, between the pleura which covers the lung (*visceral* layer), and that which lines the inner surface of the chest (*parietal* layer), is inserted in the drawing only for the sake of distinctness. These layers are, in health, everywhere in contact, one with the other; and between them is only just so much fluid as will ensure the lungs gliding easily, in their expansion and contraction, on the inner surface of the parietal layer, which lines the chest-wall. While considering the subject of normal respiration, we may discard altogether the notion of the existence of any space or cavity between the lungs and the wall of the chest.

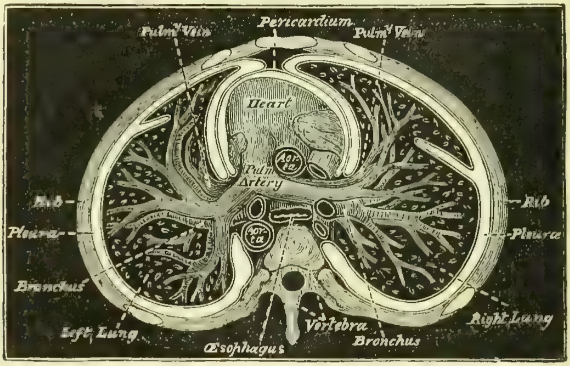

Fig. 149.—*Transverse section of the chest* (after Gray).

If, however, an opening be made so as to permit air or fluid to enter the pleural sac, the lung, in virtue of its elasticity, recoils, and a considerable space is left between the lung and the chest-wall. In other words, the natural elasticity of the lungs would cause them at all times to contract away from the ribs, were it not that the contraction is resisted by atmospheric pressure which bears only on the *inner* surface of the air-tubes and air-cells. On the admission of air into the pleural sac, atmospheric pressure bears alike on the inner and outer surfaces of the lung, and their elastic recoil is thus no longer prevented.

Structure of the Pleura and Lung.—The pulmonary pleura consists of an outer or denser layer and an inner looser tissue. The former or *pleura proper* consists of dense fibrous tissue with elastic fibres, covered by endothelium, the cells of which are large, flat, hyaline, and transparent when the lung is expanded, but become smaller, thicker, and granular when the lung collapses. In the pleura is a lymph-canalicular system; and connective tissue corpuscles are found in the fibres and tissue which forms its groundwork. The inner, looser, or subpleural tissue contains lamellæ of fibrous connective tissue and connective tissue corpuscles between them. Numerous lymphatics are to be met with, which form a dense plexus of vessels, many of which contain valves. They are simple endothelial tubes, and take origin in the lymph-canalicular system of the pleura proper. Scattered bundles of unstriped muscular fibre occur in the pulmonary pleura. They are especially strongly developed on those parts (anterior and internal surfaces of lungs) which move most freely in respiration: their function is doubtless to aid in expiration. The structure of the *parietal* portion of the pleura is very similar to that of the visceral layer.

Each lung is partially subdivided into separate portions called *lobes;* the right lung into three lobes, and the left into two. Each of these lobes, again, is composed of a large number of minute parts, called *lobules.* Each pulmonary lobule may be considered a lung in miniature, consisting, as it does, of a branch of the bronchial tube, of air-cells, blood vessels, nerves, and lymphatics, with a sparing amount of areolar tissue.

On entering a lobule, the small bronchial tube, the structure of which has been just described (*a*, fig. 150), divides and sub-divides; its walls at the same time becoming thinner and thinner, until at length they are formed only of a thin membrane of areolar and elastic tissue, lined by a layer of *squamous* epithelium, not provided with cilia. At the same time, they are altered in shape;

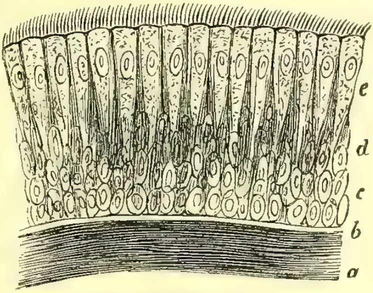

Fig. 150.—*Ciliary epithelium of the human trachea.* *a*, Layer of longitudinally arranged elastic fibres; *b*, basement membrane; *c*, deepest cells, circular in form; *d*, intermediate elongated cells; *e*, outermost layer of cells fully developed and bearing cilia. × 350. (Kölliker.)

each of the minute terminal branches widening out funnel-wise, and its walls being pouched out irregularly into small saccular dilatations, called *air-cells* (fig. 151, *b*). Such a funnel-shaped terminal branch of the bronchial tube, with its group of pouches or air-cells, has been called an *infundibulum* (figs. 151, 152), and the irregular oblong space in its centre, with which the air-cells communicate, an *intercellular passage.*

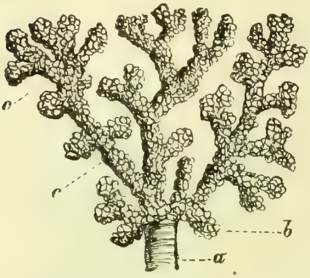

Fig. 151.—*Terminal branch of a bronchial tube, with its infundibula and air-cells*, from the margin of the lung of a monkey, injected with quicksilver. *a*, terminal bronchial twig; *b b*, infundibula and air-cells, × 10. (F. E. Schulze.)

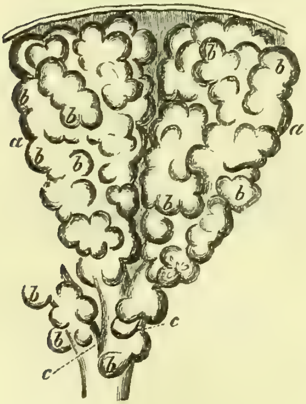

Fig. 152.—*Two small infundibula or groups of air-cells, a a*, with air-cells, *b b*, and the ultimate bronchial tubes, *c c*, with which the air-cells communicate. From a new-born child. (Kölliker.)

The air-cells, or air-vesicles, may be placed singly, like recesses from the intercellular passage, but more often they are arranged in groups or even in rows, like minute sacculated tubes; so that a short series of vesicles, all communicating with one another, open by a common orifice into the tube. The vesicles are of various forms, according to the mutual pressure to which they are subject; their walls are nearly in contact, and they vary from $\frac{1}{50}$ to $\frac{1}{70}$ of an inch in diameter. Their walls are formed of fine membrane, similar to that of the intercellular passages, and continuous with it, which membrane is folded on itself so as to form a sharp-edged border at each circular orifice of communication between contiguous air-vesicles, or between the vesicles and the bronchial passages. Numerous fibres of elastic tissue are spread out between contiguous air-cells, and many of these are attached to the outer surface of the fine membrane of which each cell is composed, imparting to it additional strength, and the power of recoil after distension. The cells are lined by a layer of epithelium (fig. 153), not provided with cilia. Outside the cells, a network of pulmonary capillaries is spread out so densely (fig. 154), that the interspaces or meshes are even narrower than the vessels, which are, on an average, $\frac{1}{3000}$ of an inch in diameter.

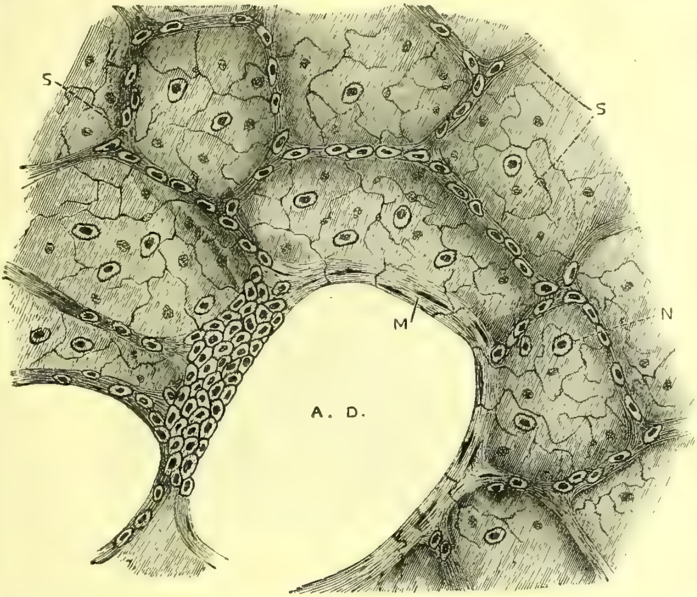

Fig. 153.—*From a section of lung of a cat, stained with silver nitrate.* **A. D.** Alveolar duct or intercellular passage. S. Alveolar septa. N. Alveoli or air-cells, lined with large flat, nucleated cells, with some smaller polyhedral nucleated cells. Circular muscular fibres are seen surrounding the interior of the alveolar duct, and at one part is seen a group of small polyhedral cells continued from the bronchus. (Klein and Noble Smith.)

Between the atmospheric air in the cells and the blood in these vessels, nothing intervenes but the thin walls of the cells and capillaries; and the exposure of the blood to the air is the more complete, because the folds of membrane between contiguous cells, and often the spaces between the walls of the same, contain only a single layer of capillaries, both sides of which are thus at once exposed to the air.

The air-vesicles situated nearest to the centre of the lung are smaller and their networks of capillaries are closer than those nearer to the circumference. The vesicles of adjacent lobules do not communicate; and those of the same lobule or proceeding from the same intercellular passage, do so as a general rule only near angles of bifurcation; so that, when any bronchial tube is closed or obstructed, the supply of air is lost for all the cells opening into it or its branches.

Blood-supply.—The lungs receive blood from two sources, (*a*) the pulmonary artery, (*b*) the bronchial arteries. The former conveys *venous* blood to the lungs for its *arterialization*, and this blood takes no share in the nutrition of the pulmonary tissues through which it passes. (*b*) The branches of the bronchial arteries ramify for nutrition's sake in the walls of the bronchi, of the larger pulmonary vessels, in the interlobular connective tissue, &c.; the blood of the bronchial vessels being returned chiefly through the bronchial and partly through the pulmonary veins.

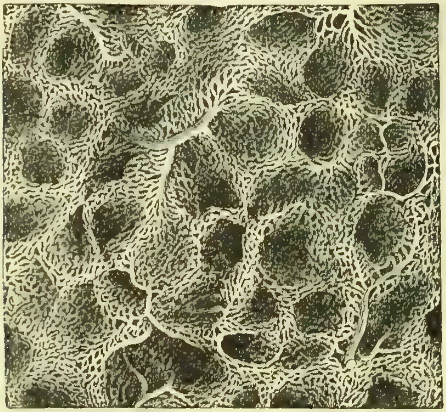

Fig. 154.—*Capillary net-work of the pulmonary blood vessels* in the human lung. × 60. (Kölliker.)

Lymphatics.—The lymphatics are arranged in three sets:—
1. Irregular lacunæ in the walls of the alveoli or air-cells. The lymphatic vessels which lead from these accompany the pulmonary vessels towards the root of the lung. 2. Irregular anastomosing spaces in the walls of the bronchi. 3. Lymph-spaces in the pulmonary pleura. The lymphatic vessels from all these irregular

sinuses pass in towards the root of the lung to reach the bronchial glands.

Nerves.—The nerves of the lung are to be traced from the anterior and posterior pulmonary plexuses, which are formed by branches of the vagus and sympathetic. The nerves follow the course of the vessels and bronchi, and in the walls of the latter many small ganglia are situated.

Mechanism of Respiration.

Respiration consists of the alternate expansion and contraction of the thorax, by means of which air is drawn into or expelled from the lungs. These acts are called **Inspiration** and **Expiration** respectively.

For the *inspiration* of air into the lungs it is evident that all that is necessary is such a movement of the side-walls or floor of the chest, or of both, that the capacity of the interior shall be enlarged. By such increase of capacity there will be of course a diminution of the pressure of the air in the lungs, and a fresh quantity will enter through the larynx and trachea to equalise the pressure on the inside and outside of the chest.

For the *expiration* of air, on the other hand, it is also evident that, by an opposite movement which shall diminish the capacity of the chest, the pressure in the interior will be increased, and air will be expelled, until the pressures within and without the chest are again equal. It both cases the air passes through the trachea and larynx, whether in entering or leaving the lungs, there being no other communication with the exterior of the body; and the lung, for the same reason, remains under all the circumstances described closely in contact with the walls and floor of the chest. To speak of expansion of the chest, is to speak also of expansion of the lung.

We have now to consider the means by which the respiratory movements are effected.

Respiratory Movements.

A. Inspiration.—The enlargement of the chest in *inspiration* is a muscular act; the effect of the action of the inspiratory muscles being an increase in the size of the chest-cavity (*a*) in the vertical, and (*b*) in the lateral and antero-posterior diameters. The muscles engaged in *ordinary* inspiration are the diaphragm; the external intercostals; parts of the internal intercostals; the levatores costarum; and serratus posticus superior.

(*a*.) The *vertical diameter* of the chest is increased by the contraction and consequent descent of the diaphragm,—the sides of the muscle descending most, and the central tendon remaining comparatively unmoved; while the intercostal and other muscles, by acting at the same time, prevent the diaphragm, during its contraction, from drawing in the sides of the chest.

(*b*.) The increase in the *lateral* and *antero-posterior diameters* of the chest is effected by the raising of the ribs, the greater number of which are attached very obliquely to the spine and sternum (see Figure of Skeleton in frontispiece).

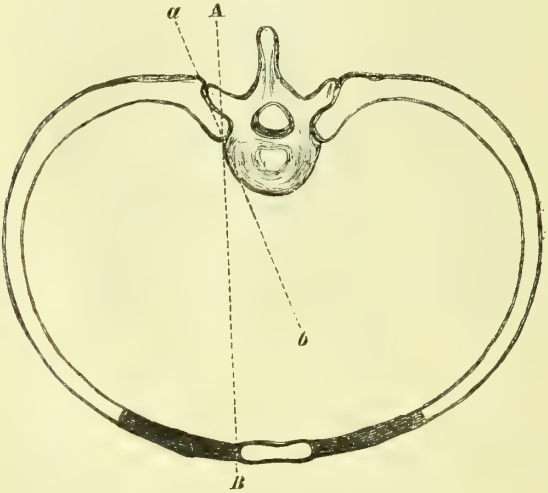

Fig. 155.—*Diagram of axes of movement of ribs.*

The elevation of the ribs takes place both in front and at the sides—the hinder ends being prevented from performing any upward movement by their attachment to the spine. The movement of the front extremities of the ribs is of necessity accompanied by an upward and forward movement of the sternum to which they are attached, the movement being greater at the lower end than at the upper end of the latter bone.

The axes of rotation in these movements are two; one corresponding with a line drawn through the two articulations which the rib forms with the spine (*a b*, fig. 155); and the other, with a line drawn from one of these (head of rib) to the sternum (A B, fig. 155, and fig. 156); the motion of the rib around the latter axis being somewhat after the fashion of raising the handle of a bucket.

The elevation of the ribs is accompanied by a slight opening out of the angle which the bony part forms with its cartilage (fig. 156, A); and thus an additional means is provided for increasing the antero-posterior diameter of the chest.

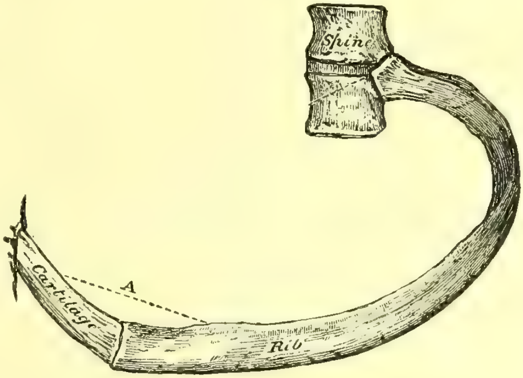

Fig. 156.—*Diagram of movement of a rib in inspiration.*

The muscles by which the ribs are raised, in *ordinary* quiet inspiration, are the *external intercostals*, and that portion of the *internal intercostals* which is situate between the costal cartilages; and these are assisted by the *levatores costarum*, and the *serratus posticus superior*. The action of the *levatores* and the *serratus* is very simple. Their fibres, arising from the spine as a fixed point, pass obliquely downwards and forwards to the ribs, and necessarily raise the latter when they contract. The action of the intercostal muscles is not quite so simple, inasmuch as, passing merely from rib to rib, they seem at first sight to have no fixed point towards which they can pull the bones to which they are attached.

A very simple apparatus will explain this apparent anomaly and make their action plain. Such an apparatus is shown in fig. 157. A B is an upright bar, representing the spine, with which are jointed two parallel bars, C and D, which represent two of the ribs, and are connected in front by moveable joints with another upright, representing the sternum.

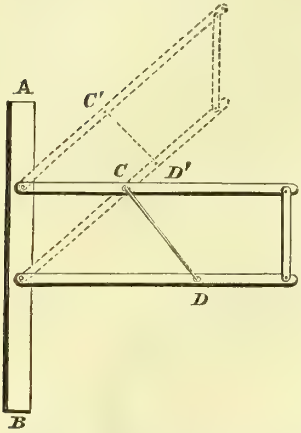

Fig. 157.—*Diagram of apparatus showing the action of the external intercostal muscles.*

If with such an apparatus elastic bands be connected in imitation of the intercostal muscles, it will be found that when stretched on the bars after the fashion of the *external* intercostal fibres (fig. 157, C D), *i.e.*, passing downwards and forwards, they raise them (fig. 157 C′ D′); while on the other hand, if placed in imitation of the position of the *internal* intercostals (fig. 158, E F), *i.e.*, passing downwards and backwards, they depress them (fig. 158, E′ F′).

The explanation of the foregoing facts is very simple. The intercostal muscles, in contracting, merely do that which all other contracting fibres do, viz., bring nearer together the points to which they are attached; and in order to do this, the external intercostals must raise the ribs, the points C and D (fig. 157) being nearer to each other when the parallel bars are in the position of the dotted lines. The limit of the movement in the apparatus is reached when the elastic band extends at right angles to the two bars which it connects—the points of attachment C′ and D′ being then at the smallest possible distance one from the other.

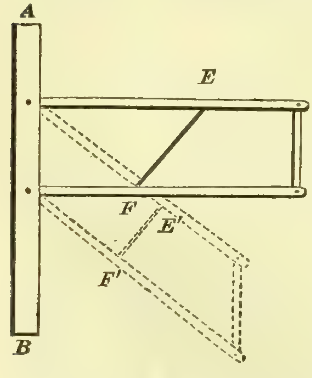

Fig. 158.—*Diagram of apparatus showing the action of the internal intercostal muscles.*

The *internal* intercostals (excepting those fibres which are attached to the cartilages of the ribs), have an opposite action to that of the external. In contracting they must pull down the ribs, because the points E and F (fig. 158) can only be brought nearer one to another (fig. 158, E′, F′) by such an alteration in their position.

On account of the oblique position of the *cartilages* of the ribs with reference to the sternum, the action of the *inter-cartilaginous* fibres of the internal intercostals must, of course, on the foregoing principles, resemble that of the external intercostals.

In tranquil breathing, the expansive movements of the lower part of the chest are greater than those of the upper. In forced inspiration, on the other hand, the greatest extent of movement appears to be in the upper antero-posterior diameter.

Muscles of Extraordinary Inspiration.—In *extraordinary* or forced inspiration, as in violent exercise, or in cases in which there is some interference with the due entrance of air into the chest, and in which, therefore, strong efforts are necessary, other muscles than those just enumerated, are pressed into the service. It is very difficult or impossible to separate by a hard and fast line, the so-called muscles of *ordinary* from those of *extraordinary* inspiration; but there is no doubt that the following are but little used as *respiratory* agents, except in cases in which unusual efforts are required—the *scaleni* muscles, the *sternomastoid*, the *serratus magnus*, the *pectorales*, and the *trapezius.*

Types of Respiration.—The expansion of the chest in inspitation presents some peculiarities in different persons. In young children, it is effected chiefly by the diaphragm, which being highly arched in expiration, becomes flatter as it contracts, and, descending, presses on the abdominal viscera, and pushes forward the front walls of the abdomen. The movement of the abdominal walls being here more manifest than that of any other part, it is usual to call this the *abdominal* type of respiration. In men, together with the descent of the diaphragm, and the pushing forward of the front wall of the abdomen, the chest and the sternum are subject to a wide movement in inspiration (*inferior costal* type). In women, the movement appears less extensive in the lower, and more so in the upper, part of the chest (*superior costal* type). (See figs. 159, 160.)

B. Expiration.—From the enlargement produced in inspiration, the chest and lungs return in ordinary tranquil expiration, by their elasticity; the force employed by the inspiratory muscles in distending the chest and overcoming the elastic resistance of the lungs and chest-walls, being returned as an expiratory effort when the muscles are relaxed. This elastic recoil of the lungs is sufficient, in ordinary quiet breathing, to expel air from the chest in the intervals of inspiration, and no muscular power is required. In all voluntary expiratory efforts, however, as in speaking, singing, blowing, and the like, and in many involuntary actions also, as sneezing, coughing, etc., something more than merely passive elastic power is necessary, and the proper expiratory muscles are brought into action. By far the chief of these are the abdominal muscles, which, by pressing on the viscera of the abdomen, push up the floor of the chest formed by the diaphragm, and by thus making pressure on the lungs, expel air from them through the trachea and larynx. All muscles, however, which depress the ribs, must act also as muscles of expiration, and therefore we must conclude that the abdominal muscles are assisted in

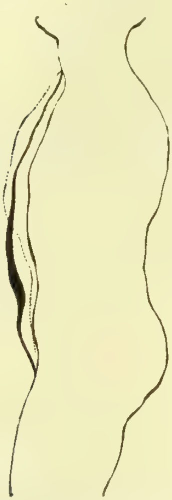

Fig. 159.—*The changes of the thoracic and abdominal walls of the male during respiration.* The back is supposed to be fixed, in order to throw forward the respiratory movement as much as possible. The outer black continuous line in front represents the ordinary breathing movement: the anterior margin of it being the boundary of inspiration, the posterior margin the limit of expiration. The line is thicker over the abdomen, since the ordinary respiratory movement is chiefly abdominal: thin over the chest, for there is less movement over that region. The dotted line indicates the movement on deep inspiration, during which the sternum advances while the abdomen recedes.

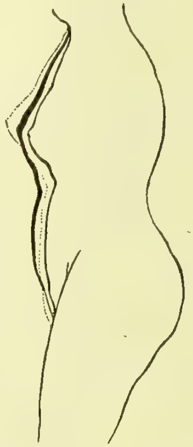

Fig. 160.—*The respiratory movement in the female.* The lines indicate the same changes as in the last figure. The thickness of the continuous line over the sternum shows the larger extent of the ordinary breathing movement over that region in the female than in the male. (John Hutchinson.)

The posterior continuous line represents in both figures the limit of forced expiration.

their action by the greater part of the *internal* intercostals, the *triangularis sterni*, the *serratus posticus inferior*, and *quadratus lumborum.* When by the efforts of the expiratory muscles, the chest has been squeezed to less than its average diameter, it again, on relaxation of the muscles, returns to the normal dimensions by virtue of its elasticity. The construction of the chest-walls, therefore, admirably adapts them for recoiling against and resisting as well undue contraction as undue dilatation.

In the natural condition of the parts, the lungs can never contract to the utmost, but are always more or less "on the stretch," being kept closely in contact with the inner surface of the walls of the chest by atmospheric pressure, and can contract away from these only when, by some means or other, as by making an opening into the pleural cavity, or by the effusion of fluid there, the pressure on the exterior and interior of the lungs becomes equal. Thus, under ordinary circumstances, the degree of contraction or dilatation of the lungs is dependent on that of the boundary walls of the chest, the outer surface of the one being in close contact with the inner surface of the other, and obliged to follow it in all its movements.

Respiratory Rhythm.—The acts of expansion and contraction of the chest, take up, under ordinary circumstances, a nearly equal time. The act of inspiring air, however, especially in women and children, is a little shorter than that of expelling it, and there is commonly a very slight pause between the end of expiration and the beginning of the next inspiration. The respiratory rhythm may be thus expressed :—

Inspiration	6
Expiration	7 or 8

A very slight **pause.**

Respiratory Sounds.—If the ear be placed in contact with the wall of the chest, or be separated from it only by a good conductor of sound, a faint *respiratory murmur* is heard during inspiration. This sound varies somewhat in different parts—being loudest or coarsest in the neighbourhood of the trachea and large bronchi (tracheal and bronchial breathing), and fading off into a faint sighing as the ear is placed at a distance from these (vesicular breathing). It is best heard in children, and in them a faint murmur is heard in expiration also. The cause of the vesicular murmur has received various explanations. Most observers hold that the sound is produced by the friction of the air against the walls of the alveoli of the lungs when they are undergoing distension (Laennec, Skoda), others that it is due to an oscillation of the current of air as it enters the alveoli (Chauveau), whilst others believe that the sound is produced in the glottis, but that it is modified in its passage to the pulmonary alveoli (Beau, Gee).

Respiratory Movements of the Nostrils and of the Glottis.—During the action of the muscles which directly draw air into the chest, those which guard the opening through which it enters are not passive. In hurried breathing the instinctive dilatation of the nostrils is well seen, although under ordinary conditions it may not be noticeable. The opening at the upper part of the larynx, however, or *rima glottidis* (fig. 297), is dilated at each inspiration, for the more ready passage of air, and becomes smaller at each expiration ; its condition, therefore, corresponding during respiration with that of the walls of the chest. There is a further likeness between the two acts in that, under ordinary circumstances, the dilatation of the rima glottidis is a muscular act, and its contraction chiefly an elastic recoil; although, under various conditions, to be hereafter mentioned, there may be, in the contraction of the glottis, considerable muscular power exercised.

Terms used to express Quantity of Air breathed.—*Breathing* or *tidal air*, is the quantity of air which is habitually and almost uniformly changed in each act of breathing. In a healthy adult man it is about 30 cubic inches.

Complemental air, is the quantity over and above this which can be drawn into the lungs in the deepest inspiration; its amount is various, as will be presently shown.

Reserve air. After ordinary expiration, such as that which expels the breathing or tidal air, a certain quantity of air remains in the lungs, which may be expelled by a forcible and deeper expiration. This is termed reserve air.

Residual air is the quantity which still remains in the lungs after the most violent expiratory effort. Its amount depends in great measure on the absolute size of the chest, but may be estimated at about 100 cubic inches.

The total quantity of air which passes into and out of the lungs of an adult, at rest, in 24 hours, is about 686,000 cubic inches. This quantity, however, is largely increased by exertion; the average amount for a hard-working labourer in the same time, being 1,568,390 cubic inches.

Respiratory Capacity.—The greatest respiratory capacity of the chest is indicated by the quantity of air which a person can expel from his lungs by a forcible expiration after the deepest inspiration that he can make; it expresses the power which a person has of breathing in the emergencies of active exercise, violence, and disease. The average capacity of an adult (at 60° F. or 15·4° C.) is about 225 cubic inches.

The *respiratory* capacity, or as Hutchinson called it, *vital* capacity, is usually measured by a modified gasometer (*spirometer* of Hutchinson), into which the experimenter breathes,—making the most prolonged expiration possible after the deepest possible inspiration. The quantity of air which is thus expelled from the lungs is indicated by the height to which the air chamber of the spirometer rises; and by means of a scale placed in connection with this, the number of cubic inches is read off.

In healthy men, the respiratory capacity varies chiefly with the stature, weight, and age.

It was found by Hutchinson, from whom most of our information on this subject is derived, that at a temperature of 60° F., 225 cubic inches is the average *vital* or respiratory capacity of a healthy person, five feet seven inches in height.

Circumstances affecting the amount of respiratory capacity.—For every inch of height above this standard the capacity is increased, on an average, by eight cubic inches; and for every inch below, it is diminished by the same amount.

The influence of *weight* on the capacity of respiration is less manifest and considerable than that of height: and it is difficult to arrive at any definite conclusions on this point, because the natural average weight of a healthy man in relation to stature has not yet been determined. As a general statement, however, it may be said that the capacity of respiration is not affected by weights under 161 pounds, or 11½ stones; but that, above this point, it is diminished at the rate of one cubic inch for every additional pound up to 196 pounds, or 14 stones.

By *age*, the capacity appears to be increased from about the fifteenth to the thirty-fifth year, at the rate of five cubic inches per year; from thirty-five to sixty-five it diminishes at the rate of about one and a half cubic inch per year; so that the capacity of respiration of a man of sixty years old would be about 30 cubic inches less than that of a man forty years old, of the same height and weight. (John Hutchinson.)

Number of Respirations, and Relation to the Pulse.—The *number* of respirations in a healthy adult person usually ranges from fourteen to eighteen per minute. It is greater in infancy and childhood. It varies also much according to different circumstances, such as exercise or rest, health, or disease, etc. Variations in the number of respirations correspond ordinarily with similar variations in the pulsations of the heart. In health the proportion is about 1 to 4, or 1 to 5, and when the rapidity of the heart's action is increased, that of the chest movement is commonly increased also; but not in every case in equal proportion. It happens occasionally in disease, especially of the lungs or air-passages, that the number of *respiratory* acts increases in quicker proportion than the beats of the *pulse;* and, in other affections, much more commonly, that the number of the pulses is greater in proportion than that of the respirations.

There can be no doubt that the number of respirations of any given animal is largely affected by its size. Thus, comparing animals of the same kind, in a tiger (lying quietly) the number of respirations was 20 per minute, while in a small leopard (lying quietly) the number was 30. In a small monkey 40 per minute; in a large baboon, 20.

The rapid, panting respiration of mice, even when quite still, is familiar, and contrasts strongly with the slow breathing of a large animal such as the elephant (eight or nine times per minute). These facts may be explained as follows:—The heat-producing power of any given animal depends largely on its bulk, while its loss of heat depends to a great extent upon the surface area of its body. If of two animals of similar shape, one be ten times as long as the other, the area of the large animal (representing its loss of heat) is 100 times that of the small one, while its bulk (representing production of heat) is about 1000 times as great. Thus in order to balance its much greater relative loss of heat, the smaller animal must have all its vital functions, circulation, respiration, &c., carried on much more rapidly.

Force of Inspiratory and Expiratory Muscles.—The force with which the inspiratory muscles are capable of acting is greatest in individuals of the height of from five feet seven inches to five feet eight inches, and will elevate a column of three inches of mercury. Above this height, the force decreases as the stature increases; so that the average of men of six feet can elevate only about two and a half inches of mercury. The force manifested in the strongest expiratory acts is, on the average, one-third greater than that exercised in inspiration. But this difference is in great measure due to the power exerted by the elastic reaction of the walls of the chest; and it is also much influenced by the disproportionate strength which the expiratory muscles attain, from their being called into use for other purposes than that of simple expiration. The force of the inspiratory act is, therefore, better adapted than that of the expiratory for testing the muscular strength of the body. (John Hutchinson.)

The instrument used by Hutchinson to gauge the inspiratory and expiratory power was a mercurial manometer, to which was attached a tube fitting the nostrils, and through which the inspiratory or expiratory effort was made. The following table represents the results of numerous experiments

Power of Inspiratory Muscles.		Power of Expiratory Muscles.
1·5 in.	Weak	2·0 in.
2·0 ,,	Ordinary	2·5 ,,
2·5 ,,	Strong	3·5 ,,
3·5 ,,	Very strong	4·5 ,,
4·5 ,,	Remarkable	5·8 ,,
5·5 ,,	Very remarkable	7·0 ,,
6·0 ,,	Extraordinary	8·5 ,,
7·0 ,,	Very extraordinary	10·0 ,,

The greater part of the force exerted in deep inspiration is employed in overcoming the resistance offered by the elasticity of the walls of the chest and of the lungs.

The amount of this elastic resistance was estimated by observing the elevation of a column of mercury raised by the return of air forced, after death, into the lungs, in quantity equal to the known capacity of respiration during life; and Hutchinson calculated, according to the well-known hydrostatic law of equality of pressures (as shown in the Bramah press), that the total force to be overcome by the muscles in the act of inspiring 200 cubic inches of air is more than 450 lbs.

The elastic force overcome in ordinary inspiration is, according to the same authority, equal to about 170 lbs.

Douglas Powell has shown that within the limits of *ordinary tranquil respiration*, the elastic resilience of the *walls of the chest* favours *inspiration;* and that it is only in deep inspiration that the ribs and rib-cartilages offer an opposing force to their dilatation. In other words, the elastic resilience of the lungs, at the end of an act of ordinary breathing, has drawn the chest-walls within the limits of their normal degree of expansion. Under all circumstances, of course, the elastic tissue of the *lungs* opposes inspiration, and favours expiration.

Functions of Muscular Tissue of Lungs.—It is possible that the contractile power which the bronchial tubes and air-vesicles possess, by means of their *muscular fibres* may (1) assist in expiration; but it is more likely that its chief purpose is (2) to regulate and adapt, in some measure, the quantity of air admitted to the lungs, and to each part of them, according to the supply of blood; (3) the muscular tissue contracts upon and gradually expels collections of mucus, which may have accumulated within the tubes, and cannot be ejected by forced expiratory efforts, owing to collapse or other morbid conditions of the portion of lung connected with the obstructed tubes (Gairdner). (4) Apart from any of the before-mentioned functions, the presence of muscular fibre in the walls of a hollow viscus, such as a lung, is only what might be expected from analogy with other organs. Subject as the lungs are to such great variation in size it might be anticipated that the elastic tissue, which enters so largely into their composition, would be supplemented by the presence of much muscular fibre also.

Respiratory Changes in the Air and in the Blood.

A. In the Air.

Composition of the Atmosphere.—The *atmosphere* we breathe has, in every situation in which it has been examined in its natural state, a nearly uniform composition. It is a mixture of oxygen, nitrogen, carbonic acid, and watery vapour, with, commonly, traces of other gases, as ammonia, sulphuretted hydrogen, &c. Of every 100 *volumes* of pure atmospheric air, 79 volumes (on an average) consist of nitrogen, the remaining 21 of oxygen. By weight the proportion is N. 75, O. 25. The proportion of carbonic acid is extremely small; 10,000 volumes of atmospheric air contain only about 4 or 5 of carbonic acid.

The quantity of watery vapour varies greatly according to the temperature and other circumstances, but the atmosphere is never without some. In this country, the average quantity of watery vapour in the atmosphere is 1·40 per cent.

Composition of Air which has been breathed.— The changes effected by respiration in the atmospheric air are: 1, an increase of temperature; 2, an increase in the quantity of carbonic acid; 3, a diminution in the quantity of oxygen; 4, a diminution of volume; 5, an increase in the amount of watery vapour; 6, the addition of a minute amount of organic matter and of free ammonia.

1. The expired air, heated by its contact with the interior of the lungs, is (at least in most climates) hotter than the inspired air. Its temperature varies between 97° and 99.5° F. (36°— 37·5° C.), the lower temperature being observed when the air has remained but a short time in the lungs. Whatever may be the temperature of the air when inhaled, it nearly acquires that of the blood before it is expelled from the chest.

2. The Carbonic Acid in respired air is always increased; but the quantity exhaled in a given time is subject to change from various circumstances. From every volume of air inspired, about 4·8 per cent. of oxygen is abstracted; while a rather smaller quantity, 4·3, of carbonic acid is added in its place: the air will contain, therefore, 434 vols. of carbonic acid in 10,000. Under ordinary circumstances, the quantity of carbonic acid exhaled into the air breathed by a healthy adult man amounts to 1346 cubic inches, or about 636 grains per hour. According to this estimate, the weight of carbon excreted from the lungs is about 173 grains per hour, or rather more than 8 ounces in twenty-four hours. These quantities must be considered approximate only, inasmuch as various circumstances, even in health, influence the amount of carbonic acid excreted, and, correlatively, the amount of oxygen absorbed.

Circumstances influencing the amount of carbonic acid excreted.—The following are the chief:—Age and sex. Respiratory movements. External temperature. Season of year. Condition of respired air. Atmospheric conditions. Period of the day. Food and drink. Exercise and sleep.

a. Age and Sex.—The quantity of carbonic acid exhaled into the air breathed by males, regularly increases from eight to thirty years of age; from thirty to fifty the quantity, after remaining stationary for awhile, gradually diminishes, and from fifty to extreme age it goes on diminishing, till it scarcely exceeds the quantity exhaled at ten years old. In females (in whom the quantity exhaled is always less than in males of the same age) the same regular increase in quantity goes on from the eighth year to the age of puberty, when the quantity abruptly ceases to increase, and remains stationary so long as they continue to menstruate. When menstruation has ceased, it soon decreases at the same rate as it does in old men.

b. Respiratory Movements.—The more quickly the movements of respiration are performed, the smaller is the proportionate quantity of carbonic acid contained in each volume of the expired air. Although, however, the proportionate quantity of carbonic acid is thus diminished during frequent respiration, yet the absolute amount exhaled into the air within a given time is increased thereby, owing to the larger quantity of air which is breathed in the time. The last half of a volume of expired air contains more carbonic acid than the half first expired; a circumstance which is explained by the one portion of air coming from the remote part of the lungs, where it has been in more immediate and prolonged contact with the blood than the other has, which comes chiefly from the larger bronchial tubes.

c. External temperature.—The observation made by Vierordt at various temperatures between 38° F. and 75° F. (3·4°—23·8° C.) show, for warm-blooded animals, that within this range, every rise equal to 10° F. causes a diminution of about two cubic inches in the quantity of carbonic acid exhaled per minute.

d. Season of the Year.—The season of the year, independently of temperature, materially influences the respiratory phenomena; spring being the season of the greatest, and autumn of the least activity of the respiratory and other functions. (Edward Smith.)

e. Purity of the Respired Air.—The average quantity of carbonic acid given out by the lungs constitutes about 4·3 per cent. of the expired air; but if the air which is breathed be previously impregnated with carbonic acid (as is the case when the same air is frequently respired), then the quantity of carbonic acid exhaled becomes much less.

f. Hygrometric State of Atmosphere.—The amount of carbonic acid exhaled is considerably influenced by the degree of moisture of the atmosphere, much more being given off when the air is moist than when it is dry. (Lehmann.)

g. Period of the Day.—During the day-time more carbonic acid is exhaled than corresponds to the oxygen absorbed; while, on the other hand, at night very much more oxygen is absorbed than is exhaled in carbonic acid. There is, thus, a *reserve fund* of oxygen absorded by night to meet the requirements of the day. If the total quantity of carbonic acid exhaled in 24 hours be represented by 100, 52 parts are exhaled during the day, and 48 at night. While, similarly, 33 parts of the oxygen are absorbed during the day, and the remaining 67 by night. (Pettenkofer and Voit.)

h. Food and Drink.—By the use of *food* the quantity is increased, whilst by fasting it is diminished; it is greater when animals are fed on farinaceous food than when fed on meat. The effects produced by spirituous drinks depend much on the kind of drink taken. Pure alcohol tends rather to increase than to lessen respiratory changes, and the amount therefore of carbonic acid expired; rum, ale, and porter, also sherry, have very similar effects. On the other hand, brandy, whisky, and gin, particularly the latter, almost always lessened the respiratory changes, and consequently the amount of carbonic acid exhaled. (Edward Smith.)

i. Exercise.—Bodily exercise, in moderation, increases the quantity to about one-third more than it is during rest: and for about an hour after exercise the volume of the air expired in the minute is increased about 118 cubic inches: and the quantity of carbonic acid about 7·8 cubic inches per minute. Violent exercise, such as full labour on the treadwheel, still further increases the amount of the acid exhaled. (Edward Smith.)

A larger quantity is exhaled when the barometer is low than when it is high.

3. The oxygen is diminished, and its diminution is generally proportionate to the increase of the carbonic acid.

For every volume of carbonic acid exhaled into the air, 1·17421 volumes of oxygen are absorbed from it, and 1346 cubic inches, or 636 grains being exhaled in the hour the quantity of oxygen absorbed in the same time is 1584 cubic inches, or 542 grains. According to this estimate, there is more oxygen absorbed than is exhaled with carbon to form carbonic acid.

4. The volume of air expired in a given time is less than that of the air inspired (allowance being made for the expansion in being heated), and that the loss is due to a portion of oxygen absorbed and not returned in the exhaled carbonic acid, all observers agree, though as to the actual quantity of oxygen so absorbed, they differ even widely. The amount of oxygen absorbed is on an average 4·8 per cent. so that the expired air contains 16·2 volumes per cent. of that gas.

The quantity of oxygen that does not combine with the carbon given off in carbonic acid from the lungs is probably disposed of in forming some of the carbonic acid and water given off from the skin, and in combining with sulphur and phosphorus to form part of the acids of the sulphates and phosphates excreted in the urine, and probably also, with the nitrogen of the decomposing nitrogenous tissues. (Bence Jones.)

The quantity of oxygen in the atmosphere surrounding animals, appears to have very little influence on the amount of this gas absorbed by them, for the quantity consumed is not greater even though an excess of oxygen be added to the atmosphere experimented with.

It has often been discussed whether *Nitrogen* is absorbed by or exhaled from the lungs during respiration. At present, all that can be said on the subject is that, under most circumstances, animals appear to expire a very small quantity above that which exists in the inspired air. During prolonged fasting, on the contrary, a small quantity appears to be absorbed.

5. The watery vapour is increased. The quantity emitted is, as a general rule, sufficient to saturate the expired air, or very nearly so. Its absolute amount is, therefore, influenced by the following circumstances, (1), by the quantity of air respired; for the greater this is, the greater also will be the quantity of moisture

exhaled. (2), by the quantity of watery vapour contained in the air previous to its being inspired; because the greater this is, the less will be the amount required to complete the saturation of the air; (3), by the temperature of the expired air; for the higher this is, the greater will be the quantity of watery vapour required to saturate the air; (4), by the length of time which each volume of inspired air is allowed to remain in the lungs; for although, during] ordinary respiration, the expired air is always saturated with watery vapour, yet when respiration is performed very rapidly the air has scarcely time to be raised to the highest temperature, or be fully charged with moisture ere it is expelled.

The quantity of water exhaled from the lungs in twenty-four hours ranges (according to the various modifying circumstances already mentioned) from about 6 to 27 ounces, the ordinary quantity being about 9 or 10 ounces. Some of this is probably formed by the chemical combination of oxygen with hydrogen in the system; but the far larger proportion of it is water which has been absorbed, as such, into the blood from the alimentary canal, and which is exhaled from the surface of the air-passages and cells, as it is from the free surfaces of all moist animal membranes, particularly at the high temperature of warm-blooded animals.

6. A small quantity of ammonia is added to the ordinary constituents of expired air. It seems probable, however, both from the fact that this substance cannot be always detected, and from its minute amount when present, that the whole of it may be derived from decomposing particles of food left in the mouth, or from carious teeth or the like; and that it is, therefore, only an accidental constituent of expired air.

7. The quantity of organic matter in the breath is about 3 grains in twenty-four hours. (Ransome.)

The following represents the kind of experiment by which the foregoing facts regarding the excretion of carbonic acid, water, and organic matter, have been established.

A bird or mouse is placed in a large bottle, through the stopper of which two tubes pass, one to supply fresh air, and the other to carry off that which has been expired. Before entering the bottle, the air is made to bubble through a strong solution of caustic potash, which absorbs the carbonic acid, and then through lime-water, which by remaining limpid, proves the absence of carbonic acid. The air which has been breathed by the animal is made to bubble through lime water, which at once becomes turbid and soon quite milky from the precipitation of calcium carbonate; and it finally passes through strong sulphuric acid, which, by turning brown, indicates the presence of organic matter. The watery vapour in the expired air will condense inside the bottle if the surface be kept cool.

By means of an apparatus sufficiently large and well constructed, experiments of the kind have been made extensively on man.

Methods by which the Respiratory Changes in the Air are effected.

The method by which fresh air is inhaled and expelled from the lungs has been considered. It remains to consider how it is that the blood absorbs oxygen from, and gives up carbonic acid to, the air of the alveoli. In the first place, it must be remembered that the tidal air only amounts to about 25—30 cubic inches at each inspiration, and that this is of course insufficient to fill the lungs, but it mixes with the stationary air by *diffusion*, and so supplies to it new oxygen. The amount of oxygen in expired air, which may be taken as the average composition of the mixed air in the lungs, is about 16 to 17 per cent.; in the pulmonary alveoli it may be rather less than this. From this air the venous blood has to take up oxygen in the proportion of 8 to 12 vols. in every hundred volumes of blood, as the difference between the amount of oxygen in arterial and venous blood is no less than that. It seems therefore somewhat difficult to understand how this can be accomplished at the low oxygen tension of the pulmonary air. But as was pointed out in a previous Chapter (IV.), the oxygen is not simply dissolved in the blood, but is to a great extent chemically combined with the hæmoglobin of the red corpuscles; and when a fluid contains a body which enters into loose chemical combination in this way with a gas, the tension of the gas in the fluid is not directly proportional to the total quantity of the gas taken up by the fluid, but to the excess above the total quantity which the substance dissolved in the fluid is capable of taking up (a known quantity in the case of hæmoglobin, viz., 1·59 cm. for one grm. hæmoglobin). On the other hand, if the substance be not saturated, *i.e.*, if it be not combined with as much of the gas as it is capable of taking up, further combination leads to no increase of its tension. However, there is a point at which the hæmoglobin gives up its oxygen when it is exposed to a low partial pressure of oxygen, and there is also a point at which it neither takes up nor gives out oxygen; in the case of arterial blood of the dog, this is found to be when the oxygen tension of the atmosphere is equal to 3·9 per cent. (or 29·6 mm. of mercury), which is equivalent to saying that the oxygen tension of arterial blood is 3·9 per cent.; venous blood, in a similar manner, has been found to have an oxygen tension of 2·8 per cent. At a higher temperature, the tension is raised, as there is a greater tendency at a high temperature for the chemical compound to undergo dissociation. It is therefore easy to see that the oxygen tension of the air of the pulmonary alveoli is quite sufficient, even supposing it much less than that of the expired air, to enable the venous blood to take up oxygen, and what is more, it will take it up until the hæmoglobin is very nearly saturated with the gas.

As regards the elimination of carbonic acid from the blood, there is evidence to show that it is given up by a process of simple diffusion, the only condition necessary for the process being that the tension of the carbonic acid of the air in the pulmonary alveoli should be less than the tension of the carbonic acid in venous blood. The carbonic acid tension of the alveolar air probably does not exceed in the dog 3 or 4 per cent., while that of the venous blood is 5·4 per cent., or equal to 41 mm. of mercury.

B. Respiratory Changes in the Blood.

Circulation of Blood in the Respiratory Organs.—To be exposed to the air thus alternately moved into and out of the air cells and minute bronchial tubes, the blood is propelled from the right ventricle through the pulmonary capillaries in steady streams, and slowly enough to permit every minute portion of it to be for a few seconds exposed to the air, with only the thin walls of the capillary vessels and the air-cells intervening. The pulmonary circulation is of the simplest kind: for the pulmonary artery branches regularly; its successive branches run in straight lines, and do not anastomose: the capillary plexus is uniformly spread over the air-cells and intercellular passages; and the veins derived from it proceed in a course as simple and uniform as that of the arteries, their branches converging but not anastomosing. The veins have no valves, or only small imperfect ones prolonged from their angles of junction, and incapable of closing the orifice of either of the veins between which they are placed. The pulmonary circulation also is unaffected by changes of atmospheric pressure, and is not exposed to the influence of the pressure of muscles: the force by which it is accomplished, and the course of the blood are alike simple.

Changes produced in the Blood by Respiration.—The most obvious change which the blood of the pulmonary artery undergoes in its passage through the lungs is 1*st*, that of **colour**, the dark crimson of venous blood being exchanged for the bright scarlet of arterial blood; 2*nd*, and in connection with the preceding change, it gains oxygen; 3*rd*, it loses carbonic acid; 4*th*, it becomes slightly cooler (p. 239); 5*th*, it coagulates sooner and more firmly, and, apparently, contains more fibrin (see p. 108). The oxygen absorbed into the blood from the atmospheric air in the lungs is combined chemically with the hæmoglobin of the red blood-corpuscles. In this condition it is carried in the arterial blood to the various parts of the body, and brought into near relation or contact with the tissues. In these tissues, and in the blood which circulates in them, a certain portion of the oxygen, which the arterial blood contains, disappears, and a proportionate quantity of carbonic acid and water is formed. The venous blood, containing the new-formed carbonic acid returns to the lungs, where a portion of the carbonic acid is exhaled, and a fresh supply of oxygen is taken in.

Mechanism of Various Respiratory Actions.—It will be well here, perhaps, to explain some respiratory acts, which appear at first sight somewhat complicated, but cease to be so when the mechanism by which they are performed is clearly understood. The accompanying diagram (fig. 161) shows that the cavity of the chest is separated from that of the abdomen by the diaphragm, which, when acting, will lessen its curve, and thus descending, will push *downwards and forwards* the abdominal viscera; while the abdominal muscles have the opposite effect, and in acting will push the viscera *upwards and backwards*, and with them the diaphragm, supposing its ascent to be not from any cause interfered with. From the same diagram it will be seen that the lungs communicate with the exterior of the body through the glottis, and further on through the mouth and nostrils—through either of them separately, or through both at the same time, according to the position of the soft palate. The stomach communicates with the exterior of the body through the œsophagus, pharynx, and mouth; while below the rectum opens at the anus, and the bladder through the urethra. All these openings, through which the hollow viscera communicate with the exterior of the body, are guarded by muscles, called sphincters, which can act independently of each other. The position of the latter is indicated in the diagram.

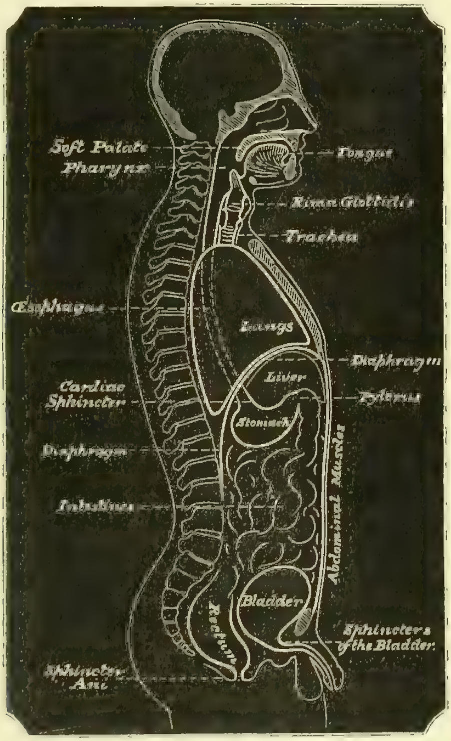

Fig. 161.

Sighing.—In sighing there is a rather prolonged inspiration; the air almost noiselessly passing in through the glottis, and by the elastic recoil of the lungs and chest-walls, and probably also of the abdominal walls, being rather suddenly expelled again.

Now, in the first, or *inspiratory* part of this act, the descent of the diaphragm presses the abdominal viscera downwards, and of course this pressure tends to evacuate the contents of such as communicate with the exterior of the body. Inasmuch, however, as their various openings are guarded by sphincter muscles, in a state of constant tonic contraction, there is no escape of their contents, and air simply enters the lungs. In the second, or *expiratory* part of the act of sighing, there is also pressure mode on the abdominal viscera in the opposite direction, by the elastic or muscular recoil of the abdominal walls; but the pressure is relieved by the escape of air through the open glottis, and the relaxed diaphragm is pushed up again into its original position. The sphincters of the stomach, rectum, and bladder, act as before.

Hiccough resembles sighing in that it is an inspiratory act; but the inspiration is sudden instead of gradual, from the diaphragm acting suddenly and spasmodically; and the air, therefore suddenly rushing through the unprepared rima glottidis, causes vibration of the vocal cords, and the peculiar sound.

Coughing.—In the act of coughing, there is most often first an inspiration, and this is followed by an expiration; but when the lungs have been filled by the preliminary inspiration, instead of the air being easily let out again through the glottis, the latter is momentarily closed by the approximation of the vocal cords, and then the abdominal muscles, strongly acting, push up the viscera against the diaphragm, and thus make pressure on the air in the lungs until its tension is sufficient to burst open noisily the vocal cords which oppose its outward passage. In this way a considerable force is exercised, and mucus or any other matter that may need expulsion from the lungs or trachea is quickly and sharply expelled by the outstreaming current of air.

Now it is evident on reference to the diagram (fig. 161), that pressure exercised by the abdominal muscles in the act of coughing, acts as forcibly on the abdominal viscera as on the lungs, inasmuch as the viscera form the medium by which the upward pressure on the diaphragm is made, and of necessity there is quite as great a tendency to the expulsion of their contents as of the air in the lungs. The instinctive, and if necessary, voluntarily increased contraction of the sphincters, however, prevents any escape at the openings guarded by them, and the pressure is effective at one part only, namely, the rima glottidis.

Sneezing.—The same remarks that apply to coughing, are almost exactly applicable to the act of sneezing; but in this instance the blast of air, on escaping from the lungs, is directed, by an instinctive contraction of the pillars of the fauces and descent of the soft palate, chiefly through the nose, and any offending matter is thence expelled.

Speaking.—In speaking, there is a voluntary expulsion of air through the glottis by means of the expiratory muscles; and the vocal cords are put, by the muscles of the larynx, in a proper position and state of tension for vibrating as the air passes over them, and thus producing sound. The sound is moulded into words by the tongue, teeth, lips, &c.—the vocal cords producing the sound only, and having nothing to do with *articulation.*

Singing.—Singing resembles speaking in the manner of its production; the laryngeal muscles, by variously altering the position and degree of tension of the vocal cords, producing the different notes. Words used in the act of singing are of course framed, as in speaking, by the tongue, teeth, lips, etc.

Sniffing.—Sniffing is produced by a somewhat quick action of the diaphragm and other inspiratory muscles. The mouth is, however, closed, and by these means the whole stream of air is made to enter by the nostrils. The alæ nasi are, commonly, at the same time, instinctively dilated.

Sobbing.—Sobbing consists in a series of convulsive inspirations, at the moment of which the glottis is usually more or less closed.

Laughing.—Laughing is a series of short and rapid expirations.

Yawning.—Yawning is an act of inspiration, but is unlike most of the preceding actions in being always more or less involuntary. It is attended by a stretching of various muscles about the palate and lower jaw, which is probably analogous to the stretching of the muscles of the limbs in which a weary man finds relief, as a voluntary act, when they have been some time out of action. The involuntary and reflex character of yawning depends probably on the fact that the muscles concerned are themselves at all times more or less involuntary, and require, therefore, something beyond the exercise of the will to set them in action. For the same reason, yawning, like sneezing, cannot be well performed voluntarily.

Sucking.—Sucking is not properly a respiratory act, but it may be most conveniently considered in this place. It is caused chiefly by the depressor muscles of the os hyoides. These, by drawing downwards and backwards the tongue and floor of the mouth, produce a partial vacuum in the latter: and the weight of the atmosphere then acting on all sides tends to produce equilibrium on the inside and outside of the mouth as best it may. The communication between the mouth and pharynx is completely shut off by the contraction of the pillars of the soft palate and descent of the latter so as to touch the back of the tongue; and the equilibrium, therefore, can be restored only by the entrance of something through the mouth. The action, indeed, of the tongue and floor of the mouth in sucking may be compared to that of the piston in a syringe, and the muscles which pull down the os hyoides and tongue, to the power which draws the handle.

Influence of the Nervous System in Respiration.—Like all other functions of the body, the discharge of which is necessary to life, respiration must be essentially an involuntary act. Else, life would be in constant danger, and would cease on the loss of consciousness for a few moments, as in sleep. But it is also necessary that respiration should be to some extent under the control of the will. For were it not so, it would be impossible to perform those voluntary respiratory acts which have been just enumerated and explained, as speaking, singing, and the like.

The respiratory movements and their rhythm, so far as they are involuntary and independent of consciousness (as on all ordinary occasions) are under the governance of a *nerve-centre* in the *medulla oblongata* corresponding with the origin of the pneumogastric nerves; that is to say, the motor nerves and through them, the muscles concerned in the respiratory movements, are excited by a stimulus which issues from this part of the nervous system. How far the medulla acts *automatically*, *i.e.*, how far the stimulus originates in it, or how far it is merely a nerve-centre for *reflex* action, is not certainly known. Probably, as will be seen, both events happen; and, in both cases, the stimulus is the result of the condition of the blood.

The respiratory centre is bilateral or double, since the respiratory movements continue after the medulla at this point is divided in the middle line.

As regards its supposed automatic action, it has been shown that if the spinal cord be divided below the medulla, and both vagi be divided so that no afferent impulses can reach it from below, the nasal and laryngeal respiration continues, and the only possible course of the afferent impulses would be through the cranial nerves; and when the cord and medulla are intact the division of these produces no effect upon respiration, so that it appears evident that the afferent stimuli are not absolutely necessary for maintaining the respiratory movements. But although automatic in its action the respiratory centre may be reflexly excited, and the chief channel of this reflex influence is the vagus nerve; for when the nerve of one side is divided, respiration is slowed, and if both vagi be cut the respiratory action is still slower.

The influence of the vagus trunk upon it is twofold, for if the nerve be divided below the origin of the superior laryngeal branch and the central end be stimulated, respiratory movements are increased in rapidity, and indeed follow one another so quickly if the stimuli be increased in number, that after a time cessation of respiration in inspiration follows from a tetanus of the respiratory muscles (diaphragm). Whereas if the superior laryngeal branch be divided, although no effect, or scarcely any, follows the mere division, on stimulation of the central end respiration is slowed, and after a time, if the stimulus be increased, stops, but not in inspiration as in the other case, but in expiration. Thus the vagus trunk contains fibres which slow and fibres which accelerate respiration. If we adopt the theory of a doubly acting respiratory centre in the floor of the medulla, one tending to produce inspiration and the other expiration, and acting in antagonism as it were, so that there is a gradual increase in the tendency to produce respiratory action, until it culminates in an inspiratory effort, which is followed by a similar action of the expiratory part of the centre, producing an expiration, we must look upon the main trunk of the vagus as aiding the inspiratory, and of the superior laryngeal as aiding the expiratory part of the centre, the first nerve possibly inhibiting the action of the expiratory centre, whilst it aids the inspiratory, and the latter nerve having the very opposite effect. But inasmuch as the respiration is slowed on division of the vagi, and not quickened or affected manifestly on simple division of the superior larygneal, it must be supposed that the vagi fibres are always in action, whereas the superior larygneal fibres are not.

It appears, however, that there are, in some animals at all events, subordinate centres in the spinal cord which are able, under certain conditions, to discharge the function of the chief medullary centre.

The centre in the medulla may be influenced not only by afferent impulses proceeding along the vagus and laryngeal nerves but also by those proceeding from the cerebrum, as well as by impressions made upon the nerves of the skin, or upon part of the fifth nerve distributed to the nasal mucous membrane, or upon other sensory nerves, as is exemplified by the deep inspiration which follows the application of cold to the surface of the skin, and by the sneezing which follows the slightest irritation of the nasal mucous membrane.

At the time of birth, the separation of the placenta, and the consequent non-oxygenation of the fœtal blood, are the circumstances which immediately lead to the issue of automatic impulses to action from the respiratory centre in the medulla oblongata. But the quickened action which ensues on the application of cold air or water, or other sudden stimulus, to the skin, shows well the intimate connection which exists between this centre and other parts which are not ordinarily connected with the function of respiration.

Methods of Stimulation of Respiratory Centre.—It is now necessary to consider the method by which the centre or centres are stimulated themselves, as well as the manner, in which the afferent vagi impulses are produced.

The more venous the blood, the more marked are the inspiratory impulses, and if the air is prevented from entering the chest, in a short time the respiration becomes very laboured. Its cessation is followed by an abnormal rapidity of the inspiratory acts, which make up even in depth for the previous stoppage. The condition caused by obstruction to the entrance of air, or by any circumstance by which the oxygen of the blood is used up in an abnormally quick manner, is known as *dyspnœa*, and as the aëration of the blood becomes more and more interfered with, not only are the ordinary respiratory muscles employed, but also those extraordinary muscles which have been previously enumerated (p. 231), so that as the blood becomes more and more venous the action of the medullary centre becomes more and more active. The question arises as to what condition of the venous blood causes this increased activity, whether it is due to deficiency of oxygen or excess of carbonic acid in the blood. This has been answered by the experiments, which show on the one hand that dyspnœa occurs when there is no obstruction to the exit of carbonic acid, as when an animal is placed in an atmosphere of nitrogen, and therefore cannot be due to the accumulation of carbonic acid, and secondly, that if plenty of oxygen be supplied, dyspnœa proper does not occur, although the carbonic acid of the blood is in excess. The respiratory centre is evidently stimulated to action by the absence of sufficient oxygen in the blood circulating in it.

The method by which the vagus is stimulated to conduct afferent impulses, influencing the action of the respiratory centre, appears to be by the venous blood circulating in the lungs, or as some say by the condition of the air in the pulmonary alveoli. And if either of these be the stimuli it will be evident that as the condition of venous blood stimulates the peripheral endings of the vagus in the lungs, the vagus action which tends to help on the discharge of inspiratory impulses from the centre, must tend also to increase the activity of the centre, when the blood in the lungs becomes more and more venous. No doubt the venous condition of the blood will affect all the sensory nerves in a similar manner, but it has been shown that the circulation of too little blood through the centre is quite sufficient by itself for the purpose; as when its blood supply is cut off increased inspiratory actions ensue.

Effects of Vitiated Air.—Ventilation.—We have seen that the air expired from the lungs contains a large proportion of carbonic acid and a minute amount of organic putrescible matter.

Hence it is obvious that if the same air be breathed again and again, the proportion of carbonic acid and organic matter will constantly increase till fatal results are produced; but long before this point is reached, uneasy sensations occur, such as headache, languor, and a sense of oppression. It is a remarkable fact that the organism after a time adapts itself to such a vitiated atmosphere, and that a person soon comes to breathe, without sensible inconvenience, an atmosphere which, when he first entered it, felt intolerable. Such an adaptation, however, can only take place at the expense of a depression of all the vital functions, which must be injurious if long continued or often repeated.

This power of adaptation is well illustrated by the experiments of Claude Bernard. A sparrow is placed under a bell-glass of such a size that it will live for three hours. If now at the end of the second hour (when it could have survived another hour) it be taken out and a fresh healthy sparrow introduced, the latter will perish instantly.

The adaptation above spoken of is a gradual and continuous one: thus a bird which will live one hour in a pint of air will live three hours in two pints; and if two birds of the same species, age, and size, be placed in a quantity of air in which either, separately, would survive three hours, they will not live 1½ hour, but only 1¼ hour.

From what has been said it must be evident that provision for a constant and plentiful supply of fresh air, and the removal of that which is vitiated, is of far greater importance than the actual cubic space per head of occupants. Not less than 2000 cubic feet per head should be allowed in sleeping apartments (barracks, hospitals, &c.), and with this allowance the air can only be maintained at the proper standard of purity by such a system of ventilation as provides for the supply of 1500 to 2000 cubic feet of fresh air per head per hour. (Parkes.)

The Effect of Respiration on the Circulation.

Inasmuch as the heart and great vessels are situated in the air-tight thorax, they are exposed to a certain alteration of pressure when the capacity of the latter is increased; for although the expansion of the lungs during inspiration tends to counter-balance this increase of area, it never quite does so, since part of the pressure of the air which is drawn into the chest through the trachea is expended in overcoming the elasticity of the lungs themselves. The amount thus used up increases as the lungs become more and more expanded, so that the pressure inside the thorax during inspiration as far as the heart and great vessels are concerned, never quite equals that outside, and at the conclusion of inspiration is considerably less than the atmospheric pressure. It has been ascertained that the amount of the pressure used up in the way above described, varies from 5 or 7 mm. of mercury during the pause, and to 30 mm. of mercury when the lungs are expanded at the end of a deep inspiration, so that it will be understood that the pressure to which the heart and great vessels are subjected diminishes as inspiration progresses. It will be understood from the accompanying diagram how, if there were no lungs in the chest, but if its capacity were increased, the effect of the increase would be expended in pumping blood into the heart from the veins, but even with the lungs placed as they are, during inspiration the pressure outside the heart and great vessels is diminished, and they have therefore a tendency to expand and to diminish the intra-vascular pressure. The diminution of pressure within the

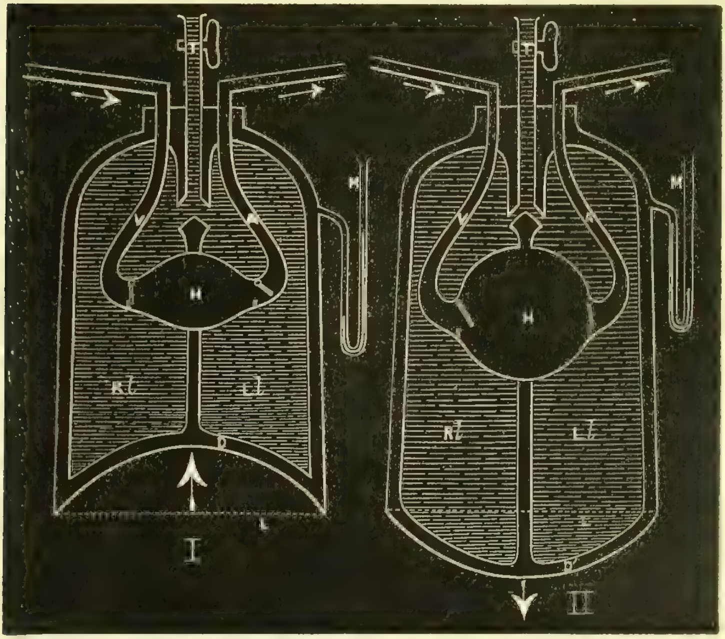

Fig. 162.—*Diagram of an apparatus illustrating the effect of inspiration upon the heart and great vessels within the thorax.*—I, the thorax at rest; II, during inspiration; D, represents the diaphragm when relaxed; D′ when contracted (it must be remembered that this position is a mere diagram), *i.e.*, when the capacity of the thorax is enlarged; H, the heart; V, the veins entering it, and A, the aorta; R*l*, L*l*, the right and left lung; T, the trachea; M, mercurial manometer in connection with the pleura. The increase in the capacity of the box representing the thorax is seen to dilate the heart as well as the lungs, and so to pump in blood through V, whereas the valve prevents reflex through A. The position of the mercury in M shows also the suction which is taking place. (Landois.)

veins passing to the right auricle and within the right auricle itself, will draw the blood into the thorax, and so assist the circulation: this suction action aiding, though independently, the suction power of the diastole of the auricle about which we have previously spoken (p. 153). The effect of sucking more blood into the right auricle will, *cæteris paribus*, increase the amount passing through the right ventricle, which also exerts a similar suction action, and through the lungs into the left auricle and ventricle and thus into the aorta, and this tends to increase the arterial tension. The effect of the diminished pressure upon the pulmonary vessels will also help towards the same end, *i.e.*, an increased flow through the lungs, so that as far as the heart and its veins are concerned inspiration increases the blood pressure in the arteries. The effect of inspiration upon the aorta and its branches within the thorax would be, however, contrary; for as the pressure outside is diminished the vessels would tend to expand, and thus to diminish the tension of the blood within them, but inasmuch as the large arteries are capable of little expansion beyond their natural calibre, the diminution of the arterial tension caused by this means would be insufficient to counteract the increase of arterial tension produced by the effect of inspiration upon the veins of the chest, and the balance of the whole action would be in favour of an increase of arterial tension during the inspiratory period. But if a tracing of the variation be taken at the same time that the respiratory movements are recorded, it will be found that, although speaking generally, the arterial tension is increased during inspiration, the maximum of arterial tension does not correspond with the acme of inspiration (fig. 163).

As regards the effect of expiration, the capacity of the chest is diminished, and the intra-thoracic pressure returns to the normal, which is not exactly equal to the atmospheric, pressure. The effect of this on the veins is to increase their intra-vascular pressure, and so to diminish the flow of blood into the left side of the heart, and with it the arterial tension, but this is almost exactly balanced by the necessary increase of arterial tension caused by the increase of the extra-vascular pressure of the aorta and large arteries, so that the arterial tension is not much affected during expiration either way. Thus, ordinary expiration does not produce a distinct obstruction to the circulation, as even when the expiration is at an end the intra-thoracic pressure is less than the extra-thoracic.

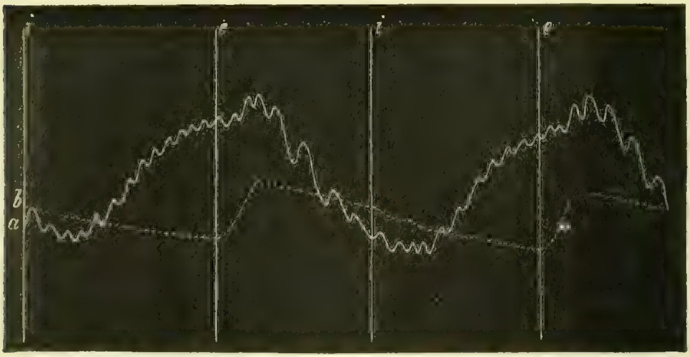

Fig. 163.—*Comparison of blood-pressure curve with curve of intra-thoracic pressure.* (*To be read from left to right.*) *a* is the curve of blood-pressure with its respiratory undulations, the slower beats on the descent being very marked; *b* is the curve of intra-thoracic pressure obtained by connecting one limb of a manometer with the pleural cavity. Inspiration begins at *i* and expiration at *e*. The intra-thoracic pressure rises very rapidly after the cessation of the inspiratory effort, and then slowly falls as the air issues from the chest; at the beginning of the inspiratory effort the fall becomes more rapid. (M. Foster.)

The effect of violent expiratory efforts, however, has a distinct action in preventing the current of blood through the lungs, as seen in the blueness of the face from congestion in straining; this condition being produced by pressure on the small pulmonary vessels.

We may summarise this mechanical effect therefore, and say that inspiration aids the circulation and so increases the arterial tension, and that although expiration does not materially aid the circulation, yet under ordinary conditions neither does it obstruct. Under extraordinary conditions, as in violent expirations, the circulation is decidedly obstructed. But we have seen that there is no exact correspondence between the points of extreme arterial tension and the end of inspiration, and we must look to the nervous system for an explanation of this apparently contradictory result.

The effect of the nervous system in producing a rhythmical alteration of the blood pressure is two-fold. In the first place the *cardio-inhibitory centre* is believed to be stimulated during the fall of blood pressure, producing a slower rate of heart-beats during expiration, which will be noticed in the tracing (fig. 163), the undulations during the decline of blood-pressure being longer but less frequent. This effect disappears when, by section of the vagi, the effect of the centre is cut off from the heart. In the

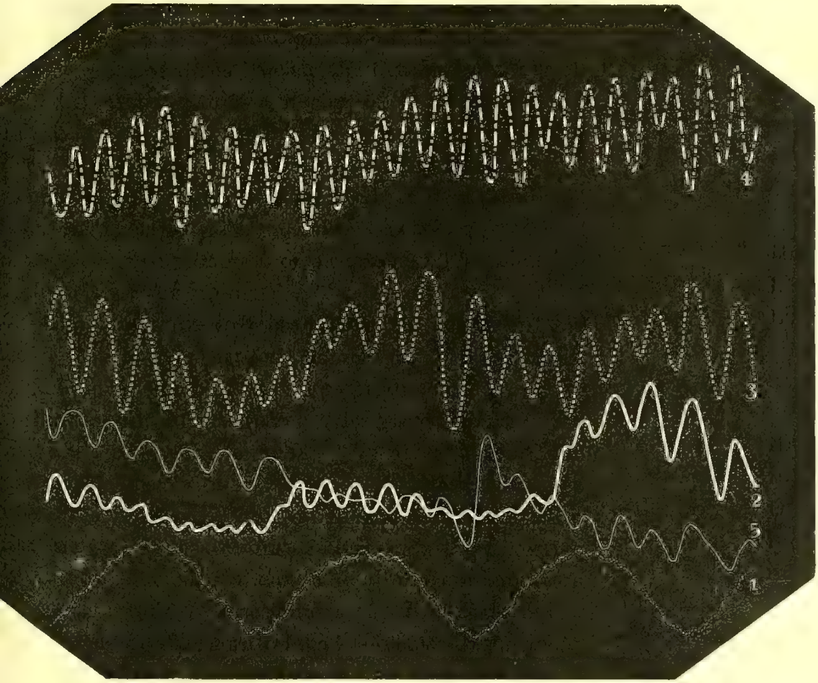

Fig. 164.—*Traube-Hering's curves.* (*To be read from left to right.*) The curves 1, 2, 3, 4, and 5 are portions selected from one continuous tracing forming the record of a prolonged observation, so that the several curves represent successive stages of the same experiment. Each curve is placed in its proper position relative to the base line, which is omitted; the blood-pressure rises in stages from 1, to 2, 3, and 4, but falls again in stage 5. Curve 1 is taken from a period when artificial respiration was being kept up, but the vagi having been divided, the pulsations on the ascent and descent of the undulations do not differ; when artificial respiration ceased these undulations for a while disappeared, and the blood-pressure rose steadily while the heart-beats became slower. Soon, as at 2, new undulations appeared; a little later, the blood-pressure was still rising, the heart-beats still slower, but the undulations still more obvious (3); still later (4), the pressure was still higher, but the heart-beats were quicker, and the undulations flatter, the pressure then began to fall rapidly (5), and continued to fall until some time after artificial respiration was resumed. (M. Foster.)

second place, the *vaso-motor centre* is also believed to send out rhythmical impulses, by which undulations of blood pressure are produced independently of the mechanical effects of respiration.

The action of the vaso-motor centre in taking part in producing rhythmical changes of blood-pressure which are called respiratory, is shown in the following way :—In an animal under the influence of urari, a record of whose blood-pressure is being taken, and where artificial respiration has been stopped, and both vagi cut, the blood-pressure curve rises at first almost in a straight line ; but after a time new rhythmical undulations occur very like the original respiratory undulations, only somewhat larger. These are called *Traube's* or *Traube-Hering's curves.* They continue whilst the blood-pressure continues to rise, and only cease when the vaso-motor centre and the heart are exhausted, when the pressure speedily falls. These curves must be dependent upon the vaso-motor centre, as the mechanical effects of respiration have been eliminated by the poison and by the cessation of artificial respiration, and the effect of the cardio-inhibitory centre be the division of the vagi. It may be presumed therefore that the vaso-motor centre, as well as the cardio-inhibitory, must be considered to take part with the mechanical changes of inspiration and expiration in producing the so-called respiratory undulations of blood-pressure.

Cheyne-Stokes' breathing.—This is a rhythmical irregularity in respirations which has been observed in various diseases, and is especially connected with fatty degeneration of the heart. Respirations occur in groups, at the beginning of each group the inspirations are very shallow, but each successive breath is deeper than the preceding until a climax is reached, then comes in a prolonged sighing expiration, succeeded by a pause, after which the next group begins.

Apnœa.—Dyspnœa.—Asphyxia.

As blood which contains a normal proportion of oxygen excites the respiratory centre (p. 252), and, as the excitement and consequent respiratory muscular movements are greater (*dyspnœa*) in proportion to the deficiency of this gas, so an abnormally large proportion of oxygen in the blood leads to diminished breathing movements, and, if the proportion be large enough, to their temporary cessation. This condition of absence of breathing is termed *apnœa*,* and it can be demonstrated, in one of the lower animals, by performing artificial respiration to the extent of saturating the blood with oxygen.

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* This term has been, unfortunately, often applied to conditions of *dyspnœa* or *asphyxia ;* but the modern application of the term, as in the text, is the more convenient.

When, on the other hand, the respiration is stopped, by, *e.g.*, interference with the passage of air to the lungs, or by supplying air devoid of oxygen, a condition ensues, which passes rapidly from the state of *dyspnœa* (difficult breathing) to what is termed *asphyxia;* and the latter quickly ends in death.

The ways by which this condition of asphyxia may be produced are very numerous; as, for example, by the prevention of the due entry of oxygen into the blood, either by direct obstruction of the trachea or other part of the respiratory passages, or by introducing instead of ordinary air a gas devoid of oxygen, or, again, by interference with the due interchange of gases between the air and the blood.

Symptoms of Asphyxia.—The most evident symptoms of asphyxia or suffocation are well known. Violent action of the respiratory muscles and, more or less, of all the muscles of the body; lividity of the skin and all other vascular parts, while the veins are also distended, and the tissues seem generally gorged with blood; convulsions, quickly followed by insensibility, and death.

The conditions which accompany these symptoms are—

(1) More or less interference with the passage of the blood through the pulmonary blood-vessels.

(2) Accumulation of blood in the right side of the heart and in the systemic veins.

(3) Circulation of impure (non-aërated) blood in all parts of the body.

Cause of Death from Asphyxia.—The causes of these conditions and the manner in which they act, so as to be incompatible with life, may be here briefly considered.

(1) The obstruction to the passage of blood through the lungs is not so great as it was once supposed to be; and such as there is occurs chiefly in the later stages of asphyxia, when, by the violent and convulsive action of the expiratory muscles, pressure is indirectly made on the lungs, and the circulation through them is proportionately interfered with.

(2) Accumulation of blood, with consequent distension of the right side of the heart and systemic veins, is the direct result, at

least in part, of the obstruction to the pulmonary circulation just referred to. Other causes, however, are in operation. (*a*) The vaso-motor centres stimulated by blood deficient in oxygen, causes contraction of all the small arteries with increase of arterial tension, and as an immediate consequence the filling of the systemic veins. (*b*) The increased arterial tension is followed by inhibition of the action of the heart, and, thus, the latter, contracting less frequently, and gradually enfeebled also by deficient supply of oxygen, becomes over-distended by blood which it cannot expel. At this stage the left as well as the right cavities are distended with blood.

The ill effects of these conditions are to be looked for partly in the heart, the muscular fibres of which, like those of the urinary bladder or any other hollow muscular organ, may be paralysed by over-stretching; and partly in the venous congestion, and consequent interference with the function of the higher nerve-centres, especially the medulla oblongata.

(3) The passage of non-aërated blood through the lungs and its distribution over the body are events incompatible with life, in one of the higher animals, for more than a few minutes; the rapidity with which death ensues in asphyxia being due, more particularly, to the effect of non-oxygenized blood on the medulla oblongata, and, through the coronary arteries, on the muscular substance of the heart. The excitability of both nervous and muscular tissue is dependent on a constant and large supply of oxygen, and, when this is interfered with, is rapidly lost. The diminution of oxygen, it may be here remarked, has a more direct influence in the production of the usual symptoms of asphyxia than the increased amount of carbonic acid. Indeed, the fatal effect of a gradual accumulation of the latter in the blood, if a due supply of oxygen be maintained, resembles rather that of a narcotic poison.

In some experiments performed by a committee appointed by the Medico-Chirurgical Society to investigate the subject of *Suspended Animation*, it was found that, in the dog, during simple asphyxia, *i.e.*, by simple privation of air, as by plugging the trachea, the average duration of the respiratory movements after the animal had been deprived of air, was 4 minutes 5 seconds; the extremes being 3 minutes 30 seconds, and 4 minutes 40 seconds. The average duration of the heart's action, on the other hand, was 7 minutes 11 seconds; the extremes being 6 minutes 40 seconds, and

7 minutes 45 seconds. It would seem, therefore, that on an average, the heart's action continues for 3 minutes 15 seconds after the animal has ceased to make respiratory efforts. A very similar relation was observed in the rabbit. Recovery never took place after the heart's action had ceased.

The results obtained by the committee on the subject of *drowning* were very remarkable, especially in this respect, that whereas an animal may recover, after simple deprivation of air for nearly four minutes, yet, after submersion in water for 1½ minute, recovery seems to be impossible. This remarkable difference was found to be due, not to the mere submersion, nor directly to the struggles of the animal, nor to depression of temperature, but to the two facts, that in drowning, a free passage is allowed to air out of the lungs, and a free entrance of water into them. It is probably to the entrance of water into the lungs that the speedy death in drowning is mainly due. The results of *post-mortem* examination strongly support this view. On examining the lungs of animals deprived of air by plugging the trachea, they were found simply congested; but in the animals drowned, not only was the congestion much more intense, accompanied with ecchymosed points on the surface and in the substance of the lung, but the air tubes were completely choked up with a sanious foam, consisting of blood, water, and mucus, churned up with the air in the lungs by the respiratory efforts of the animal. The lung-substance, too, appeared to be saturated and sodden with water, which, stained slightly with blood, poured out at any point where a section was made. The lung thus sodden with water was heavy (though it floated), doughy, pitted on pressure, and was incapable of collapsing. It is not difficult to understand how, by such infarction of the tubes, air is debarred from reaching the pulmonary cells; indeed the inability of the lungs to collapse on opening the chest is a proof of the obstruction which the froth occupying the air-tubes offers to the transit of air.

We must carefully distinguish the asphyxiating effect of an insufficient supply of oxygen from the directly poisonous action of such a gas as carbonic oxide, which is present to a considerable amount in common coal-gas. The fatal effects often produced by this gas (as in accidents from burning charcoal stoves in small, close rooms), are due to its entering into combination with the hæmoglobin of the blood-corpuscles (p. 117), and thus expelling the oxygen.

CHAPTER VII.

FOOD.

In order that life may be maintained it is necessary that the body should be supplied with food in proper quality and quantity.

The food taken in by the animal body is used for the purpose of replacing the waste of the tissues. And to arrive at a reasonable estimation of the proper diet in twenty-four hours it is necessary to consider the amount of the excreta daily eliminated from the body. The excreta contain chiefly carbon, hydrogen, oxygen, and nitrogen, but also to a less extent, sulphur, phosphorus, chlorine, potassium, sodium, and certain other of the elements. Since this is the case it must be evident that, to balance this waste, foods must be supplied containing all these elements to a certain degree, and some of them, viz., those which take the principal part in forming the excreta, in large amount. We have seen in the last Chapter that carbonic acid and ammonia, *i.e.*, the elements carbon, oxygen, nitrogen, hydrogen, are given off from the lungs. By the excretion of the kidneys—the urine—many elements are discharged from the blood, especially nitrogen, hydrogen, and oxygen. In the sweat, the elements chiefly represented are carbon, hydrogen, and oxygen, and also in the fæces. By all the excretions large quantities of water are got rid of daily, but chiefly by the urine.

The relations between the amounts of the chief elements contained in these various excreta in twenty-four hours may be represented in the following way (Landois):

——	Water.	C.	H.	N.	O.
By the lungs . .	330	248·8	—	?	651·15
By the skin . .	660	2·6	—	—	7·2
By the urine . .	1700	9·8	3·3	15·8	11·1
By the fæces . .	128	20·	3·	3·	12·
Grammes . .	2818	281·2	6·3	18·8	681·41

To this should be added 296· grammes water, which are produced by the union of hydrogen and oxygen in the body during the process of oxydation (*i.e.*, 32·89 hydrogen and 263-41 oxygen). There are twenty-six grammes of salts got rid of by the urine and six by the fæces. As the water can be supplied as such, the losses of carbon, nitrogen, and oxygen are those to which we should direct our attention in supplying food.

For the sake of example, we may now take only two elements, carbon and nitrogen, and, if we discover what amount of these is respectively discharged in a given time from the body, we shall be in a position to judge what kind of food will most readily and economically replace their loss.

The quantity of carbon daily lost from the body amounts to about 281·2 grammes or nearly 4,500 grains, and of nitrogen 18·8 grammes or nearly 300 grains; and if a man could be fed by these elements, as such, the problem would be a very simple one; a corresponding weight of charcoal, and, allowing for the oxygen in it, of atmospheric air, would be all that is necessary. But an animal can live only upon these elements when they are arranged in a particular manner with others, in the form of an organic compound, as albumen, starch, and the like; and the relative proportion of carbon to nitrogen in either of these compounds alone, is, by no means, the proportion required in the diet of man. Thus, in albumen, the proportion of carbon to nitrogen is only as 3·5 to 1. If, therefore, a man took into his body, as food, sufficient albumen to supply him with the needful amount of carbon, he would receive more than four times as much nitrogen as he wanted; and if he took only sufficient to supply him with nitrogen, he would be starved for want of carbon. It is plain, therefore, that he should take with the albuminous part of his food, which contains so large a relative amount of nitrogen in proportion to the carbon he needs, substances in which the nitrogen exists in much smaller quantities relatively to the carbon.

It is therefore evident that the diet must consist of several substances, not of one alone, and we must therefore turn to the available food-stuffs. For the sake of convenience they may be classified as follows:

A. ORGANIC.

I. **Nitrogenous**, consisting of *Proteids*, *e.g.* albumen, casein, syntonin, gluten, legumin and their allies; and *Gelatins*, which include gelatin, elastin, and chondrin. All of these contain carbon, hydrogen, oxygen, and nitrogen, and some in addition, phosphorus and sulphur.

II. **Non-Nitrogenous**, comprising:

(1.) *Amyloid or saccharine bodies*, chemically known as carbo-hydrates, since they contain carbon, hydrogen, and oxygen, with the last two elements in the proportion to form water, *i.e.*, H_2O. To this class belong starch and sugar.

(2.) *Oils and fats.*—These contain carbon, hydrogen, and oxygen; but the oxygen is less in amount than in the amyloids and saccharine bodies.

B. INORGANIC.

I. **Mineral and saline matter.**

II. **Water.**

To supply the loss of nitrogen and carbon, it is found by experience that it is necessary to combine substances which contain a large amount of nitrogen with others in which carbon is in considerable amount; and although, without doubt, if it were possible to relish and digest one or other of the above-mentioned proteids when combined with a due quantity of an amyloid to supply the carbon, such a diet, together with salt and water, ought to support life; yet we find that for the purposes of ordinary life this system does not answer, and instead of confining our nitrogenous foods to one variety of substance we obtain it in a large number of allied substances, for example, in flesh, of bird, beast, or fish; in eggs; in milk; and in vegetables. And, again, we are not content with one kind of material to supply the carbon necessary for maintaining life, but seek more, in bread, in fats, in vegetables, in fruits. Again, the fluid diet is seldom supplied in the form of pure water, but in beer, in wines, in tea and coffee, as well as in fruits and succulent vegetables.

Man requires that his food should be *cooked*. Very few organic substances can be properly digested without previous exposure to heat and to other manipulations which constitute the process of cooking. It will be well, therefore, to consider the composition of the various substances employed as food, and then to consider how they are affected by cooking.

A.—Foods containing principally nitrogenous bodies.

I.—*Flesh of Animals*, especially of the ox (beef, veal), sheep (mutton, lamb), pig (pork, bacon, ham).

Of these, beef is richest in nitrogenous matters, containing about 20 per cent., whereas mutton contains about 18 per cent., veal, 16·5, and pork, 10; the flesh is also firmer, more satisfying, and is supposed to be more strengthening than mutton, whereas the latter is more digestible. The flesh of young animals, such as lamb and veal, is less digestible and less nutritious. Pork is comparatively indigestible, and contains a large amount of fat.

Flesh contains:—(1) Nitrogenous bodies: *myosin*, *serum-albumin*, *gelatin* (from the interstitial fibrous connective tissue); *elastin* (from the elastic tissue), as well as *hæmoglobin.* (2) Fatty matters, including *lecithin* and *cholesterin.* (3) Extractive matters, some of which are agreeable to the palate, *e.g.*, *osmazome*, and others which are weakly stimulating, *e.g.*, *kreatin.* Besides, there are *sarcolactic* and *inositic acids*, *taurin*, *xanthin*, and others. (4) Salts, chiefly of potassium, calcium, and magnesium. (5) Water, the amount of which varies from 15 per cent. in dried bacon to 39 in pork, 51 to 53 in fat beef and mutton, to 72 per cent. in lean beef and mutton. (6) A certain amount of carbo-hydrate material is found in the flesh of some animals, in the form of *inosite*, *dextrin*, *grape sugar*, and (in young animals) *glycogen.*

TABLE OF PER-CENTAGE COMPOSITION OF BEEF, MUTTON, PORK, AND VEAL.—(LETHEBY.)

	Water.	Albumen.	Fat.	Salts.
Beef.—Lean	72	19·3	3·6	5·1
„ *Fat*	51	14·8	29·8	4·4
Mutton.—Lean	72	18·3	4·9	4·8
„ *Fat*	53	12·4	31·1	3·5
Veal	63	16·5	15·8	4·7
Pork.—Fat	39	9·8	48·9	2·3

Together with the flesh of the above-mentioned animals, that of the *deer*, *hare*, *rabbit*, and *birds*, constituting *venison*, *game*, and *poultry*, should be added as taking part in the supply of nitrogenous substances, and also *fish*—salmon, eels, &c., and *shell-fish*, *e.g.*, lobster, crab, mussels, oysters, shrimps, scollop, cockles, &c.

TABLE OF PER-CENTAGE COMPOSITION OF POULTRY AND FISH.—(LETHEBY.)

	Water.	Albumen.	Fats.	Salts.
Poultry	74	21	3·8	1·2

(Singularly devoid of fat, and so generally eaten with bacon or pork.)

White Fish	78	18·1	2·9	1·
Salmon	77	16·1	5·5	1·4
Eels (very rich in fat)	75	9·9	13·8	1·3
Oysters	75·74	11·72	2·42	2·73

Even now the list of fleshy foods is not complete, as nearly all animals have been occasionally eaten, and we may presume that the average composition of all is nearly the same.

II. *Milk*—Is intended as the entire food of young animals, and as such contains, when pure, all the elements of a typical diet. (1) Albuminous substances in the form of *casein* and, in small amount, of *serum-albumin*. (2) Fats in the cream. (3) Carbohydrates in the form of *lactose* or milk sugar. (4) Salts, chiefly *calcium phosphate;* and (5) Water. From it we obtain (*a*) *cheese*, which is the casein precipitated with more or less fat according as the cheese is made of skim milk, (skim cheese), of fresh milk with its cream (Cheddar and Cheshire), or of fresh milk plus cream (Stilton and double Gloucester). The precipitated casein is allowed to ripen, by which process some of the albumen is split up with formation of fat. (β) *Cream*, which consists of the fatty globules incased in casein, and which being of low specific gravity float to the surface. (γ) *Butter*, or the fatty matter deprived of its casein envelope by the process of churning. (δ) *Butter-milk*, or the fluid obtained from cream after butter has been formed; very rich therefore in nitrogen. (ϵ) *Whey*, or the fluid which remains after the precipitation of casein; this contains sugar, salt, and a small quantity of albumen.

TABLE OF COMPOSITION OF MILK, BUTTER-MILK, CREAM, AND CHEESE.—(LETHEBY AND PAYEN.)

	Nitrogenous matters.	Fats.	Lactose.	Salts.	Water.
Milk (Cow) . . .	4·1	3·9	5·2	·8	86
Buttermilk . .	4·1	·7	6·4	·8	88
Cream	2·7	26·7	2·8	1·8	66
Cheese.—Skim . .	44·8	6·3	—	4·9	44
„ *Cheddar* . .	28·4	31·1	—	4·5	36
			Non-nitrogenous matter and loss.		
„ *Neufchatel (Fresh)*	8·	40·71	36·58	·51	36·58

III. *Eggs.*—The yelk and albumen of eggs are in the same relation as food for the embryoes of oviparous animals that milk is to the young of mammalia, and afford another example of the natural admixture of the various alimentary principles.

TABLE OF THE PER-CENTAGE COMPOSITION OF FOWLS' EGGS.

	Nitrogenous substances.	Fats.	Salts.	Water.
White	20·4	—	1·6	78
Yelk	16·	30·7	1·3	52

IV. *Leguminous fruits* are used by vegetarians, as the chief source of the nitrogen of the food. Those chiefly used are *peas, beans, lentils*, &c., they contain a nitrogenous substance called *legumin*, allied to albumen. They contain about 25·30 per cent. of this nitrogenous body, and twice as much nitrogen as wheat.

B. Substances supplying principally carbohydrate bodies.

a. *Bread*, made from the ground grain obtained from various so-called *cereals*, viz., wheat, rye, maize, barley, rice, oats, &c., is the direct form in which the carbohydrate is supplied in an ordinary diet. Flour, however, besides the starch, contains *gluten*, a nitrogenous body, and a small amount of fat.

TABLE OF PER-CENTAGE COMPOSITION OF BREAD AND FLOUR.

	Nitrogenous matters.	Carbo-hydrates.	Fats.	Salts.	Water.
Bread	8·1	51·	1·6	2·3	37
Flour	10·8	70·85	2·	1·7	15

Various articles of course are made from flour, *e.g.*, macaroni, biscuits, &c., besides bread.

β. *Vegetables*, especially potatoes.

γ. *Fruits* contain sugar, and organic acids, tartaric, malic, citric, and others.

C. Substances supplying principally fatty bodies.

The chief are *butter*, *lard* (pig's fat), *suet* (beef and mutton fat).

D. Substances supplying the salts of the food.

Nearly all the foregoing substances in A, B, and C, contain a greater or less amount of the salts required in food; but green vegetables and fruit supply certain salts, without which the normal health of the body is not maintained.

E. Liquid foods.

Water is consumed alone, or together with certain other substances used to flavour it, *e.g.*, tea, coffee, &c. Tea in moderation is a stimulant, and contains an aromatic oil to which it owes its peculiar aroma, an astringent of the nature of tannin, and an alkaloid, *theine*. The composition of coffee is very nearly similar to that of tea. Cocoa, in addition to similar substances contained in tea and coffee, contains fat, albuminous matter, and starch, and must be looked upon more as a food.

Beer, in various forms, is an infusion of *malt* (barley which has sprouted, and in which the starch is converted in great part into sugar), boiled with hops and allowed to ferment. Beer contains from 1·2 to 8·8 per cent. of alcohol.

Cider and Perry, the fermented juice of the apple and pear.

Wine, the fermented juice of the grape, contains from 6 or 7 (Rhine wines, and white and red Bordeaux) to 24—25 (ports and sherries) per cent. of alcohol.

Spirits, obtained from the distillation of fermented liquors. They contain upwards of 40—70 per cent. of absolute alcohol.

Effects of cooking upon Food.—In general terms this may be said to make food more easily digestible, and this includes two other alterations, food is made more agreeable to the palate and also more pleasing to the eye. Cooking consists in exposing the food to various degrees of heat, either to the direct heat of the fire, as in roasting, or to the indirect heat of the fire, as in broiling, baking, or frying, or to hot water, as in boiling or stewing. The effect of heat upon flesh is to coagulate the albumen and colouring matter, to solidify fibrin, and to gelatinize tendons and fibrous connective tissue. Previous beating or bruising (as with steaks and chops, or keeping (as in the case of game), renders the meat more tender. Prolonged exposure to heat also develops on the surface certain empyreumatic bodies, which are agreeable both to the taste and smell. By placing meat into hot water, the external coating of albumen is coagulated, and very little, if any, of the constituents of the meat are lost afterwards if boiling be prolonged, but if the constituents of the meat are to be extracted, it should be exposed to prolonged simmering at a much lower temperature, and the "*broth*" will then contain the gelatin and extractive matters of the meat, as well as a certain amount of albumen. The addition of salt will help to extract the myosin.

The effect of boiling upon an egg coagulates the albumen, and helps in rendering the article of food more suitable for adult dietary. Upon milk, the effect of heat is to produce a scum composed of serum-albumin and a little casein (the greater part of the casein being uncoagulated) with some fat. Upon vegetables, the cooking produces the necessary effect of rendering them softer, so that they can be more readily broken up in the mouth; it also causes the starch to swell up and burst, and so aids the digestive fluids to penetrate into their substance. The albuminous matters are coagulated, and the gummy, saccharine and saline matters are removed. The conversion of flour into bread is effected by mixing it with water, a little salt and a certain amount of yeast, which consists of the cells of an organised ferment (*Torula cerevisiæ*). By the growth of this plant, which lives upon the sugar produced from the starch of the flour, carbonic acid gas and a small amount of alcohol are formed. It is by means of the former that the *dough* rises. Another method consists in mixing the flour with water containing a large quantity of the gas in solution.

By the action of heat during baking the dough continues to expand, and the gluten being coagulated, the bread sets as a permanently vesiculated mass.

I.—Effects of an insufficient diet.

Hunger and Thirst.—The sensation of *hunger* is manifested in consequence of deficiency of food in the system. The mind refers the sensation to the stomach; yet since the sensation is relieved by the introduction of food either into the stomach itself, or into the blood through other channels than the stomach, it would appear not to depend on the state of the stomach alone. This view is confirmed by the fact, that the division of both pneumogastric nerves, which are the principal channels by which the brain is cognisant of the condition of the stomach, does not appear to allay the sensations of hunger. But that the stomach has some share in this sensation is proved by the relief afforded, though only temporarily, by the introduction of even non-alimentary substances into this organ. It may, therefore, be said that the sensation of hunger is caused both by a want in the system generally, and also by the condition of the stomach itself, by which condition, of course, its own nerves are more directly affected.

The sensation of *thirst*, indicating the want of fluid, is referred to the fauces, although, as in hunger, this is, in great part, only the local declaration of a general condition. For thirst is relieved for only a very short time by moistening the dry fauces; but may be relieved completely by the introduction of liquids into the blood, either through the stomach, or by injections into the blood-vessels, or by absorption from the surface of the skin or the intestines. The sensation of thirst is perceived most naturally whenever there is a disproportionately small quantity of water in the blood: as well, therefore, when water has been abstracted from the blood, as when saline or any solid matters have been abundantly added to it. And the cases of hunger and thirst are not the only ones in which the mind derives, from certain organs, a peculiar predominant sensation of some condition affecting the whole body. Thus, the sensation of the "necessity of breathing," is referred especially to the air-passages; but, as Volkmann's experiments show, it depends on the condition of the blood which circulates everywhere, and is felt even after the lungs of animals are removed; for they continue, even then, to gasp and manifest the sensation of want of breath.

Starvation.—The effects of total deprivation of food have been made the subject of experiments on the lower animals, and have been but too frequently illustrated in man. (1.) One of the most notable effects of starvation, as might be expected, is *loss of* *weight;* the loss being greatest at first, as a rule, but afterwards not varying very much, day by day, until death ensues. Chossat found that the ultimate proportional loss was, in different animals experimented on, almost exactly the same; death occurring when the body had lost two-fifths (forty per cent.) of its original weight. Different parts of the body lose weight in very different proportions. The following results are taken, in round numbers, from the table given by M. Chossat:—

Fat	loses	93	per cent.
Blood		75	,,
Spleen		71	,,
Pancreas		64	,,
Liver		52	,,
Heart		44	,,
Intestines		42	,,
Muscles of locomotion		42	,,
Stomach		39	,,
Pharynx, Œsophagus		34	,,
Skin		33	,,
Kidneys		31	,,
Respiratory apparatus		22	,,
Bones		16	,,
Eyes		10	,,
Nervous system		2	,, (nearly).

(2.) The effect of starvation on the temperature of the various animals experimented on by Chossat was very marked. For some time the *variation* in the daily temperature was more marked than its absolute and continuous diminution, the daily fluctuation amounting to 5° or 6° F. (3° C.), instead of 1° or 2° F. (·5° to 1° C.), as in health. But a short time before death, the temperature fell very rapidly, and death ensued when the loss had amounted to about 30° F. (16·5° C.) It has been often said, and with truth, although the statement requires some qualification, that death by starvation is really death by cold; for not only has it been found that differences of time with regard to the period of the fatal result are attended by the same ultimate loss of heat, but the effect of the application of external warmth to animals cold and dying from starvation, is more effectual in reviving them than the administration of food. In other words, an animal exhausted by deprivation of nourishment is unable so to digest food as to use it as fuel, and therefore is dependent for heat on its supply from without. Similar facts are often observed in the treatment of exhaustive diseases in man.

(3.) The symptoms produced by starvation in the human subject are hunger, accompanied, or it may be replaced by pain, referred to the region of the stomach; insatiable thirst; sleeplessness; general weakness and emaciation. The exhalations both from the lungs and skin are fetid, indicating the tendency to decomposition which belongs to badly-nourished tissues; and death occurs, sometimes after the additional exhaustion caused by diarrhœa, often with symptoms of nervous disorder, delirium or convulsions.

(4.) In the human subject death commonly occurs within six to ten days after total deprivation of food. But this period may be considerably prolonged by taking a very small quantity of food, or even water only. The cases so frequently related of survival after many days, or even some weeks, of abstinence, have been due either to the last-mentioned circumstances, or to others no less effectual, which prevented the loss of heat and moisture. Cases in which life has continued after total abstinence from food and drink for many weeks, or months, exist only in the imagination of the vulgar.

(5.) The appearances presented after death from starvation are those of general wasting and bloodlessness, the latter condition being least noticeable in the brain. The stomach and intestines are empty and contracted, and the walls of the latter appear remarkably thinned and almost transparent. The various secretions are scanty or absent, with the exception of the bile, which, somewhat concentrated, usually fills the gall-bladder. All parts of the body readily decompose.

II.—Effects of Improper Diet.

Experiments on Feeding.—Experiments illustrating the ill effects produced by feeding animals upon one or two alimentary substances only have been often performed.

Dogs were fed exclusively on *sugar and distilled water*. During the first seven or eight days they were brisk and active, and took their food and drink as usual; but in the course of the second week, they began to get thin, although their appetite continued good, and they took daily between six and eight ounces of sugar. The emaciation increased during the third week, and they became feeble, and lost their activity and appetite. At the same time an ulcer formed on each cornea, followed by an escape of the humours of the eye: this took place in repeated experiments. The animals still continued to eat three or four ounces of sugar daily; but became at length so feeble as to be incapable of motion, and died on a day varying from the thirty-first to the thirty-fourth. On dissection, their bodies presented all the appearances produced by death from starvation; indeed, dogs will live almost the same length of time without any food at all.

When dogs were fed exclusively on *gum*, results almost similar to the above ensued. When they were kept on *olive-oil and water*, all the phenomena produced were the same, except that no ulceration of the cornea took place; the effects were also the same with butter. The experiments of Chossat and Letellier prove the same; and in men, the same is shown by the various diseases to which those who consume but little nitrogenous food are liable, and especially by the affection of the cornea which is observed in Hindus feeding almost exclusively on rice. But it is not only the non-nitrogenous substances, which, taken alone, are insufficient for the maintenance of health. The experiments of the Academies of France and Amsterdam were equally conclusive that *gelatin* alone soon ceases to be nutritive.

Savory's observations on food confirm and extend the results obtained by Magendie, Chossat, and others. They show that animals fed exclusively on non-nitrogenous diet speedily emaciate and die, as if from starvation; that life is much more prolonged in those fed with nitrogenous than by those with non-nitrogenous food; and that animal heat is maintained as well by the former as by the latter—a fact which proves, if proof were wanting—that nitrogenous elements of food, as well as non-nitrogenous, may be regarded as calorifacient.

III.—Effect of Too Much Food.

Sometimes the excess of food is so great that it passes through the alimentary canal, and is at once got rid of by increased peristaltic action of the intestines. In other cases, the unabsorbed portions undergo putrefactive changes in the intestines, which are accompanied by the production of gases, such as carbonic acid, carburetted and sulphuretted hydrogen; a distended condition of the bowels, accompanied by symptoms of indigestion, is the result. An excess of the substances required as food may however undergo absorption. It is a well-known fact that numbers of people habitually eat too much; especially of nitrogenous food. Dogs can digest an immense amount of meat if fed often, and the amount of meat taken by some men would supply not only the nitrogen, but the carbon which is requisite for an ordinary natural diet. A method of getting rid of an excess of nitrogen is provided by the digestive processes in the duodenum, to be presently described, whereby the excess of the albuminous food is capable of being changed before absorption into nitrogenous crystalline matters, easily converted by the liver into urea, and so easily excreted by the kidneys, affording one variety of what is called *luxus consumption;* but after a time the organs, especially the liver, will yield to the strain of the over-work, and will not reduce the excess of nitrogenous material into urea, but into other less oxidised products, such as uric acid; and general plethora and gout may be the result. This state of things, however, is delayed for a long time, if not altogether obviated, when large meat-eaters take a considerable amount of exercise.

Excess of carbohydrate food produces an accumulation of fat, which may not only be an inconvenience by causing obesity, but may interfere with the proper nutrition of muscles, causing a feebleness of the action of the heart, and other troubles. The accumulation of fat is due to the excess of carbohydrate being stored up by the protoplasm in the form of fat. Starches when taken in great excess are almost certain to give rise in addition to dyspepsia, with acidity and flatulence. There is a limit to the absorption of starch and of fat, as, if taken beyond a certain amount, they appear unchanged in the fæces.

Requisites of a Normal Diet.—It will have been understood that it is necessary that a normal diet should be made up of various articles, that they should be well cooked, and should contain about the same amount of the carbon and nitrogen that are got rid of by the excreta. Without doubt these desiderata may be satisfied in numerous ways, and it would be simply absurd to believe that the diet of every adult should be exactly similar. The age, sex, strength, and circumstances of each individual should ultimately determine his diet. A dinner of bread and hard cheese with an onion contain all the requisites for a meal; but such diet would be suitable only for those possessing strong digestive powers. It is a well-known fact that the diet of the continental nations differs from that of our own country, and that of cold from that of hot climates; but the same principle underlies them all, viz., replacement of the loss of the excreta in the most convenient and economical way possible. Without going into detail in the matter, it may be said that anyone in active work requires more nitrogenous matter than one at rest, and that children and women require less than adult men.

The quantity of food for a healthy adult man of average height and weight may be stated in the following table :—

TABLE OF WATER AND FOOD REQUIRED FOR A HEALTHY ADULT.
(PARKES.)

	In laborious occupation.	At rest.
Nitrogenous substances, *e.g.*, flesh .	6 to 7 oz. av.	2·5 oz.
Fats	3·5 to 4·5 oz.	1 oz.
Carbo-hydrates	16 to 18 oz.	12 oz.
Salts	1·2 to 1·5 oz.	·5 oz.
	26·7 to 31 oz.	16 oz.

The above is the dry food; but as this is nearly always combined with 50 to 60 per cent. of water, these numbers should be doubled, and they would then be 52 to 60 oz., and 32 oz. of so called solid food, and to this should be added 50 to 80 oz. of fluid.

Full diet scale for an adult male in hospital (*St. Bartholomew's Hospital*).

Breakfast.—1 pint of tea (with milk and sugar), bread and butter.
Dinner.—½lb. of cooked meat, ½lb. potatoes, bread and beer.
Tea.—1 pint of tea, bread and butter.
Supper.—Bread and butter, beer.

Daily allowance to each patient.—2 pints of tea, with milk and sugar; 14 oz. bread; ½ lb. of cooked meat: ½ lb. potatoes: 2 pints of beer, 1 oz. butter. 31 oz. solid, and 4 pints (80 oz.), liquid.

CHAPTER VIII.

DIGESTION.

THE object of digestion is to prepare the food to supply the waste of the tissues, which we have seen is its proper function in the economy. Few of the articles of diet are taken in the exact condition in which it is possible for them to be absorbed into the system by the blood vessels and lymphatics, without which absorption they would be useless for the purposes they have to fulfil; almost the whole of the food undergoes various changes before it is fit for absorption. Having been received into the mouth, it is subjected to the action of the teeth and tongue, and is mixed with the first of the digestive juices—the *saliva.* It is then swallowed, and, passing through the pharynx and œsophagus into the stomach, is subjected to the action of the *gastric juice.* Thence it passes into the intestines, where it meets with the bile, the pancreatic juice and the intestinal juices, all of which exercise an influence upon that portion of the food not absorbed from the stomach. By this time most of the food is capable of absorption, and the residue of undigested matter leaves the body in the form of fæces by the anus.

The course of the food through the alimentary canal of man will be readily seen from the accompanying diagram (fig. 165).

The Mouth is the cavity contained between the jaws and inclosed by the cheeks laterally, and by the lips in front; behind it opens into the pharynx by the *fauces*, and is separated from the nasal cavity by the hard palate in front, and the soft palate behind, which form its roof. The tongue forms the lower part or floor. In the jaws are contained the teeth; and when the mouth is shut these form its anterior and lateral boundaries. The whole of the mouth is lined with mucous membrane, covered by stratified squamous epithelium, which is continuous in front along the lips with the epithelium of the skin, and posteriorly with that of the pharynx. The mucous membrane is provided with numerous glands (small tubular), called mucous glands, and into it open the ducts of the salivary glands, three chief glands on each side. The tongue is not only a prehensile organ, but is also the chief seat of the sense of taste.

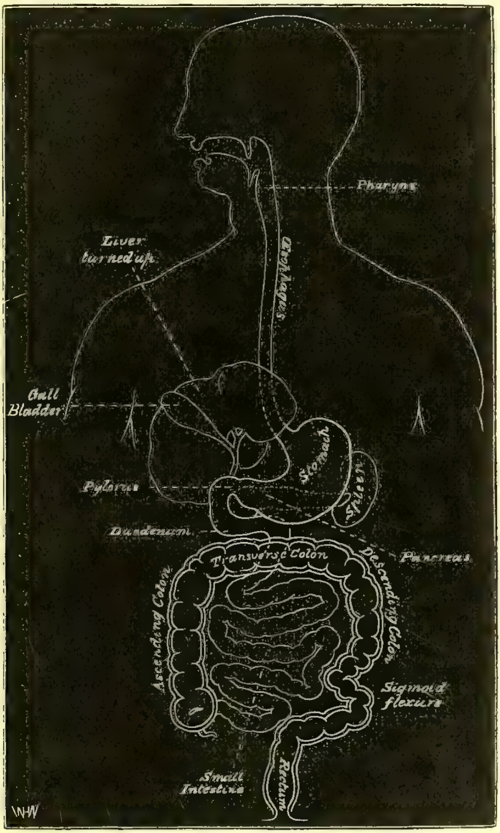

Fig. 165.—*Diagram of the Alimentary Canal.* The *small* intestine of man is from about 3 to 4 times as long as the *large* intestine.

We shall now consider, in detail, the process of digestion, as it takes place in each stage of this journey of the food through the alimentary canal.

Mastication.—The act of chewing or mastication is performed by the biting and grinding movement of the lower range of teeth against the upper. The simultaneous movements of the tongue and cheeks assist partly by crushing the softer portions of the food against the hard palate, gums, &c., and thus supplementing the action of the teeth, and partly by returning the morsels of food to the action of the teeth, again and again, as they are squeezed out from between them, until they have been sufficiently chewed.

The simple up and down, or *biting* movements of the lower jaw, are performed by the *temporal*, *masseter*, and *internal pterygoid* muscles, the action of which in closing the jaws alternates with that of the *digastric* and other muscles passing from the os hyoides to the lower jaw, which open them. The *grinding* or side to side movements of the lower jaw are performed mainly by the *external pterygoid* muscles, the muscle of one side acting alternately with the other. When both external pterygoids act together, the lower jaw is pulled directly forwards, so that the lower incisor teeth are brought in front of the level of the upper.

Temporo-maxillary Fibro-cartilage.—The function of the inter-articular fibro-cartilage of the temporo-maxillary joint in mastication may be here mentioned. (1) As an elastic pad, it serves well to distribute the pressure caused by the exceedingly powerful action of the masticatory muscles. (2) It also serves as a joint-surface or socket for the condyle of the lower jaw, when the latter has been partially drawn forward out of the glenoid cavity of the temporal bone by the external pterygoid muscle, some of the fibres of the latter being attached to its front surface, and consequently drawing it forward with the condyle which moves on it.

Nerve-mechanism of mastication.—As in the case of so many other actions, that of mastication is partly voluntary and partly reflex and involuntary. The consideration of such *sensori-motor* actions will come hereafter (see Chapter on the Nervous System). It will suffice here to state that the nerves chiefly concerned are the *sensory* branches of the fifth and the glosso-pharyngeal, and the *motor* branches of the fifth and the ninth (hypoglossal) cerebral nerves. The nerve-centre through which the reflex action occurs, and by which the movements of the various muscles are harmonised, is situate in the medulla oblongata. In so far as mastication is voluntary or mentally perceived, it becomes so under the influence, in addition to the medulla oblongata, of the cerebral hemispheres.

Insalivation.—The act of mastication is much assisted by the saliva which is secreted by the salivary glands in largely increased amount during the process, and the intimate incorporation of which with the food, as it is being chewed, is termed *insalivation.*

The Salivary Glands.

The salivary glands are the *parotid*, the *sub-maxillary*, and the *sub-lingual*, and numerous smaller bodies of similar structure, and with separate ducts, which are scattered thickly beneath the mucous membrane of the lips, cheeks, soft palate, and root of the tongue.

Structure.—The salivary glands are usually described as compound tubular glands. They are made up of lobules. Each lobule consists of the branchings of a subdivision of the main duct of the gland, which are generally more or less convoluted towards their extremities, and sometimes, according to some observers, sacculated or pouched. The convoluted or pouched portions form the *alveoli*, or proper secreting parts of the gland. The alveoli are composed of a basement membrane of flattened cells

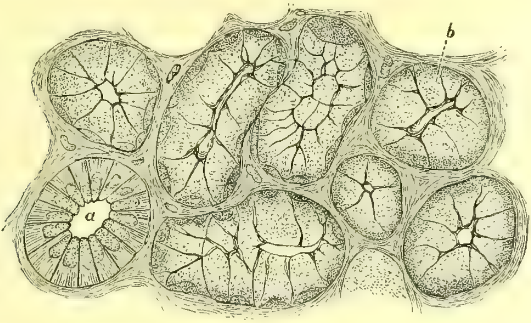

Fig. 166.—*Section of submaxillary gland of dog.* Showing gland-cells, *b*, and a duct, *a*, in section. (Kölliker.)

joined together by processes to produce a fenestrated membrane, the spaces of which are occupied by a homogeneous ground-substance. Within, upon this membrane, which forms the tube, the nucleated salivary secreting cells, of cubical or columnar form, are arranged parallel to one another surrounding a middle central canal. The granular appearance which is frequently seen in the salivary cells is due to the very dense network of fibrils which they contain. When isolated, the cells not unfrequently are found to be branched. Connecting the alveoli into lobules is a considerable amount of fibrous connective tissue, which contains both flattened and granular protoplasmic cells, lymph corpuscles, and in some cases fat cells. The lobules are connected to form larger lobules (lobes), in a similar manner. The alveoli pass into the intralobular ducts by a narrowed portion (intercalary), lined with flattened epithelium with elongated nuclei. The intercalary ducts pass into the intralobular ducts by a narrowed neck, lined with cubical cells with small nuclei. The intralobular duct is larger in size, and is lined with large columnar nucleated cells, the parts of which, towards the lumen of the tube presents a fine longitudinal striation, due to the arrangement of the cell network. It is most marked in the submaxillary gland. The intralobular ducts pass into the larger ducts, and these into the main duct of the gland. As these ducts become larger they acquire an outside coating of connective tissue, and later on some unstriped muscular fibres. The lining of the larger ducts consists of one or more layers of columnar epithelium, containing an intracellular network of fibres arranged longitudinally.

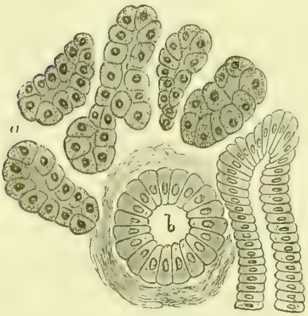

Fig. 167.—*From a section through a true salivary gland.* *a*, the gland alveoli, lined with albuminous "salivary cells;" *b*, intralobular duct cut transversely. (Klein and Noble Smith.)

Varieties.—Certain differences in the structure of salivary glands may be observed according as the glands secrete pure saliva, or saliva mixed with mucus, or pure mucus, and therefore the glands have been classified as: (1) *True salivary glands* (called most unfortunately by some *serous* glands), *e.g.*, the parotid of man and other animals, and the submaxillary of the rabbit and guinea-pig (fig. 167). In this kind the alveolar lumen is small, and the cells lining the tubule are short, granular columnar cells, with nuclei presenting the intranuclear network. During rest the cells become larger, highly granular, with obscured nuclei, and the lumen becomes smaller. During activity, and after stimulation of the sympathetic, the cells become smaller and their contents more opaque; the granules first of all disappearing from the outer part of the cells, and then being found only at the extreme inner part and contiguous border of the cell. The nuclei reappear, as does also the lumen. (2) In *the true mucus-secreting glands*, as the sublingual of man and other animals, and in the submaxillary of the dog, the tubes are larger, contain a larger lumen and also have larger cells lining them. The cells are of two kinds, (*a*) *mucous or central cells*, which are transparent columnar cells with nuclei near the basement membrane. The cell substance is made up of a fine network, which in the resting state contains a transparent substance called *mucigen*, during which the cell does not stain well with logwood (fig. 168). When the gland is secreting, *mucigen* is converted into *mucin*, and the cells swell up, appear more transparent, and stain deeply in logwood (fig. 169). During rest, the cells become smaller and more granular from having discharged their contents, and the nuclei appear more distinct. (*b*) *Semilunes of Heidenhain* (fig. 168), which are crescentic masses of granular parietal cells found here and there between the basement membrane and the central cells. These cells are small, and have a very dense reticulum, the nuclei are spherical, and increase in size during secretion. In the mucous gland there

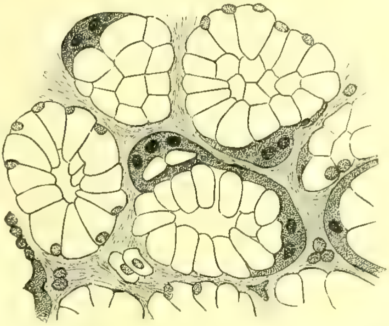

Fig. 168.—*From a section through a mucous gland in a quiescent state.* The alveoli are lined with transparent mucous cells, and outside these are the demilunes of Heidenhain. The cells should have been represented as more or less granular. (Heidenhain.)

are some large tubes, lined with large transparent central cells, and have besides a few granular parietal cells; other small tubes are lined with small granular parietal cells alone; and a third variety are lined equally with each kind of cell. (3) In the muco-salivary or mixed glands, as the human submaxillary gland, part of the gland presents the structure of the mucous gland, whilst the remainder has that of the salivary glands proper.

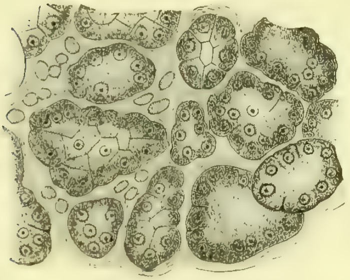

Fig. 169.—*A part of a section through a mucous gland after prolonged electrical stimulation.* The alveoli are lined with small granular cells. (Lavdovski.)

Nerves and blood-vessels.—Nerves of large size are found in the salivary glands, they are contained in the connective tissue of the alveoli principally, and in certain glands, especially in the dog, are provided with ganglia. Some nerves have special endings in Pacinian corpuscles, some supply the blood-vessels, and others, according to Pflüger, penetrate the basement membrane of the alveoli and enter the salivary cells.

The blood-vessels form a dense capillary network around the ducts of the alveoli, being carried in by the fibrous trabeculæ between the alveoli, in which also begin the lymphatics by lacunar spaces.

Saliva.—Saliva, as it commonly flows from the mouth, is mixed with the secretion of the *mucous glands*, and often with air bubbles, which, being retained by its viscidity, make it frothy. When obtained from the parotid ducts, and free from mucus, saliva is a transparent watery fluid, the specific gravity of which varies from 1004 to 1008, and in which, when examined with the microscope, are found floating a number of minute particles, derived from the secreting ducts and vesicles of the glands. In the impure or mixed saliva are found, besides these particles, numerous epithelial scales separated from the surface of the mucous membrane of the mouth and tongue, and the so-called salivary corpuscles, discharged probably from the mucous glands of the mouth and the tonsils, which, when the saliva is collected in a deep vessel, and left at rest, subside in the form of a white opaque matter, leaving the supernatant salivary fluid transparent and colourless, or with a pale bluish-grey tint. In *reaction*, the saliva, when first secreted appears to be always alkaline. During fasting, the saliva, although secreted alkaline, shortly becomes neutral; and it does so especially when secreted slowly and allowed to mix with the acid mucus of the mouth, by which its alkaline reaction is neutralized.

Chemical Composition of Mixed Saliva (Frerichs).

Water	994·10
Solids	5·90
Ptyalin	1·41
Fat	0·07
Epithelium and Proteids (including Serum-Albumin, Globulin, Mucin, &c.)	2·13
Salts :—	
Potassium Sulpho-Cyanate	2·29
Sodium Phosphate	
Calcium Phosphate	
Magnesium Phosphate	
Sodium Chloride	
Potassium Chloride	
	5·90

The presence of potassium sulphocyanate (or *thiocyanate*) (C N K S) in saliva, may be shown by the blood-red colouration which the fluid gives with a solution of ferric chloride ($Fe._2Cl._6$), and which is bleached on the addition of a solution of mercuric chloride ($HgCl_2$).

Rate of Secretion and Quantity.—The rate at which saliva is secreted is subject to considerable variation. When the tongue and muscles concerned in mastication are at rest, and the nerves of the mouth are subject to no unusual stimulus, the quantity secreted is not more than sufficient, with the mucus, to keep the mouth moist. During actual secretion the flow is much accelerated.

The *quantity* secreted in twenty-four hours varies; its average amount is probably from 1 to 3 pints (1 to 2 litres).

Uses of Saliva.—The purposes served by saliva are (1) mechanical and (2) chemical. I. *Mechanical.*—(1) It keeps the mouth in a due condition of moisture, facilitating the movements of the tongue in speaking, and the mastication of food. (2) It serves also in dissolving sapid substances, and rendering them capable of exciting the nerves of taste. But the principal mechanical purpose of the saliva is, (3) that by mixing with the food during mastication, it makes it a soft pulpy mass, such as may be easily swallowed. To this purpose the saliva is adapted both by quantity and quality. For, speaking generally, the quantity secreted during feeding is in direct proportion to the dryness and hardness of the food. The quality of saliva is equally adapted to this end. It is easy to see how much more readily it mixes with most kinds of food than water alone does; and the saliva from the parotid, labial, and other small glands, being more aqueous than the rest, is that which is chiefly *braided* and mixed with the food in mastication; while the more viscid mucous secretion of the submaxillary, palatine, and tonsillitic glands is spread over the surface of the softened mass, to enable it to slide more easily through the fauces and œsophagus. II. *Chemical.*—Saliva has the power of converting starch into glucose or grape-sugar. When saliva, or a portion of a salivary gland, is added to starch paste in a test-tube, and the mixture kept at a temperature of 100° F. (37·8° C.), the starch is very rapidly transformed into grape-sugar. There is an intermediate stage in which a part or the whole of the starch becomes dextrin.

Test for Glucose.—In such an experiment the presence of sugar is at once discovered by the application of Trommer's test, which consists in the addition of a drop or two of a solution of copper sulphate, followed by a larger quantity of caustic potash. When the liquid is boiled, an orange-red precipitate of copper suboxide indicates the presence of sugar; and when common raw starch is masticated and mingled with saliva, and kept with it at a temperature of 90° or 100° F. (30°—37·8° C.), the starch-grains are cracked or eroded, and their contents are transformed in the same manner as the starch-paste.

Saliva from the parotid is less viscid, less alkaline, clearer, and more watery than that from the submaxillary. It has, moreover, a less powerful action on starch. Sublingual saliva is the most viscid, and contains more solids than either of the other two, but does not appear to be so powerful in its action.

The salivary glands of children do not become functionally active till the age of 4 to 6 months, and hence the bad effect of feeding them before this age on starchy food, corn-flour, &c., which they are unable to render soluble and capable of absorption.[1]

Action of Saliva on Starch.—This action is due to the presence in the saliva of the body called *ptyalin*. It is a nitrogenous body, and belongs to the order of *ferments*, which are bodies whose exact chemical composition is unknown, and which are capable of producing by their presence changes in other bodies, without themselves undergoing change. Ptyalin is called a *hydrolytic ferment*, that is to say, it acts by adding a molecule of water to the body changed. The reaction is supposed to be as follows:

$$\underset{\text{Starch}}{3\,C_6H_{10}O_5} + \underset{\text{Water}}{3\,H_2O} = \underset{\text{Glucose}}{C_6H_{12}O_6} + \underset{\text{Dextrin}}{2\,(C_6H_{10}O_5)} + 2\,H_2O = \underset{\text{Glucose.}}{3\,C_6H_{12}O_6}.$$

But it is not unlikely that the action is by no means so simple. In the first place, recent observers believe that a molecule of starch must be represented by a much more complex formula; next, that the stages in the reaction are more numerous and extensive; and thirdly, that the product of the reaction is not true glucose, but *maltose*. Maltose is a sugar more akin to cane- than grape-sugar, of very little sweetening power, and with less reducing power over copper salts. Its formula is $C_{12}H_{22}O_{11}$.

The action of saliva on starch is facilitated by: (*a*) Moderate heat, about 100° F. (37·8° C.). (*b*) A slightly alkaline medium. (*c*) Removal of the changed material from time to time. Its action is retarded by: (*a*) Cold; a temperature of 32° F. (0° C.) stops it for a time, but does not destroy it, whereas a high temperature above 140° F. (60° C.) destroys it. (*b*) Acids or strong alkalies either delay or stop the action altogether. (*c*) Presence of too much of the changed material. Ptyalin, in that it converts starch into sugar, is an *amylolytic* ferment.

Starch appears to be the only principle of food upon which saliva acts chemically: it has no apparent influence on any of the other ternary principles, such as sugar, gum, cellulose, or on fat, and seems to be equally destitute of power over albuminous and gelatinous substances.

Influence of the Nervous System.—The secretion of saliva is under the control of the nervous system. It is a reflex action, and in ordinary conditions is excited by the stimulation of the peripheral branches of two nerves, viz., the *gustatory or lingual* branch of the inferior maxillary division of the fifth nerve, and the *glosso-pharyngeal* part of the eighth pair of nerves, which are distributed to the mucous membrane of the tongue and pharynx.

The stimulation occurs on the introduction of sapid substances into the mouth, and the secretion is brought about in the following way. From the terminations of these sensory nerves in the mucous membrane an impression is conveyed upwards (afferent) to the special nerve centre situated in the medulla, which controls the process, and by it is reflected to certain nerves supplied to the salivary glands, which will be presently indicated. In other words, the centre, stimulated to action by the sensory impressions carried to it, sends out impulses along efferent or secretory nerves supplied to the salivary glands, which cause the saliva to be secreted by and discharged from the gland cells. Other stimuli, however, besides that of the food, and other sensory nerves besides those mentioned, may produce reflexly the same effects. Saliva may be caused to flow by irritation of the mucous membrane of the mouth with mechanical, chemical, electrical, or thermal stimuli, also by the irritation of the mucous membrane of the stomach in some way, as in nausea, which precedes vomiting, when some of the peripheral fibres of the *vagi* are irritated. Stimulation of the *olfactory* nerves by smell of food, of the *optic* nerves by the sight of it, and of the *auditory* nerves by the sounds which are known by experience to accompany the preparation of a meal, may also, in the hungry, stimulate the nerve centre to action. In addition to these, as a secretion of saliva follows the movement of the muscles of mastication, it may be assumed that this movement stimulates the secreting nerve fibres of the gland, directly or reflexly. From the fact that the flow of saliva may be increased or diminished by mental emotions, it is evident that impressions from the cerebrum also are capable of stimulating the centre to action or of inhibiting its action.

Secretion may be excited by direct stimulation of the centre in the medulla.

A. On the Submaxillary Gland.—The submaxillary gland has been the gland chiefly employed for the purpose of experimentally demonstrating the influence of the nervous system upon the secretion of saliva, because of the comparative facility with which, with its blood-vessels and nerves, it may be exposed to view in the dog, rabbit, and other animals. The chief nerves supplied to the gland are: (1) the *chorda tympani*, a branch given off from the *facial* portio dura of the seventh pair of nerves), in the canal through which it passes in the temporal bone, in its passage from the interior of the skull to the face; and (2) branches of the *sympathetic* nerve from the plexus around the facial artery and its branches to the gland. The chorda (fig. 170, *ch. t.*), after quitting the temporal bone, passes downwards and forwards, under cover of the external pterygoid muscle, and joins at an acute angle the lingual or gustatory nerve, proceeds with it for a short distance, and then passes along the submaxillary gland duct (fig. 170, *sm.d.*), to which it is distributed, giving branches to the submaxillary ganglion (fig. 170, *sm. gl.*), and sending others to terminate in the superficial muscle of the tongue. If this nerve be exposed and divided anywhere in its course from its exit from the skull to the gland, the secretion, if the gland be in action, is arrested, and no stimulation either of the lingual or of the glosso-pharyngeal will produce a flow of saliva. But if the peripheral end of the divided nerve be stimulated, an abundant secretion of saliva ensues, and the blood supply is enormously increased, the arteries being dilated. The veins even pulsate, and the blood contained within them is more arterial than venous in character.

When, on the other hand, the stimulus is applied to the *sympathetic* filaments (mere division producing no apparent effect), the arteries contract, and the blood stream is in consequence much diminished; and from the veins, when opened, there escapes only a sluggish stream of dark blood. The saliva, instead of being abundant and watery, becomes scanty and tenacious. If both chorda tympani and sympathetic branches be divided, the gland, released from nervous control, secretes continuously and abundantly (*paralytic* secretion).

The abundant secretion of saliva, which follows stimulation of the chorda tympani, is not merely the result of a filtration of fluid from the blood-vessels, in consequence of the largely increased circulation through them. This is proved by the fact that, when the main duct is obstructed, the pressure within may considerably exceed the blood-pressure in the arteries, and also that when into the veins of the animal experimented upon some *atropin* has been previously injected, stimulation of the peripheral end of the divided chorda produces all the vascular effects as before, without any secretion of saliva accompanying them. Again, if an animal's head be cut off, and the chorda be rapidly exposed and stimulated with an interrupted current, a secretion of saliva ensues for a short time, although the blood supply is necessarily absent. These experiments serve to prove that the chorda contains two sets of nerve fibres, one set (*vaso-dilator*) which, when stimulated, act upon a local vaso-motor centre for regulating the blood supply, inhibiting its action, and causing the vessels to dilate, and so producing an increased supply of blood to the gland; while another set, which are paralyzed by injection of atropin, directly stimulate the cells themselves to activity, whereby they secrete and discharge the constituents of the saliva which they produce. These latter fibres very possibly terminate in the salivary cells themselves. If, on the other hand, the sympathetic fibres be divided, stimulation of the tongue by sapid substances, or of the trunk of the lingual, or of the glosso-pharyngeal continues to produce a flow

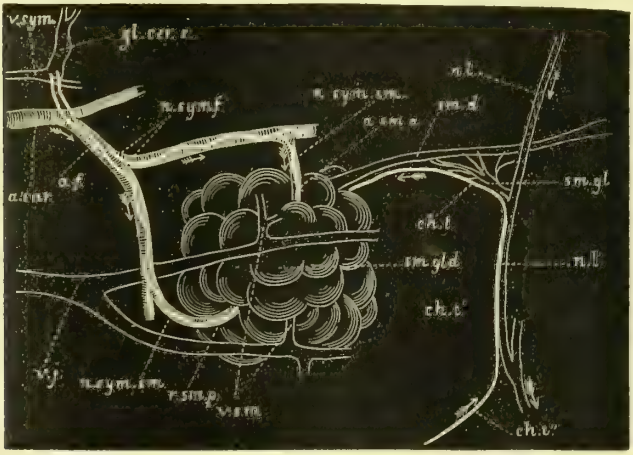

Fig. 170.—*Diagrammatic representation of the submaxillary gland of the dog with its nerves and blood-vessels.* (This is not intended to illustrate the exact anatomical relations of the several structures.) *sm. gld.*, the submaxillary gland into the duct (*sm. d.*), of which a cannula has been tied. The sublingual gland and duct are not shown. *n. l.*, *n. l'.*, the lingual or gustatory nerve; *ch. t.*, *ch. t'.*, the chorda tympani proceeding from the facial nerve, becoming conjoined with the lingual at *n. l'.*, and afterwards diverging and passing to the gland along the duct; *sm. gl.*, submaxillary ganglion with its roots; *n. l.*, the lingual nerve proceeding to the tongue; *a. car.*, the carotid artery, two branches of which, *a. sm. a.* and *r. sm. p.*, pass to the anterior and posterior parts of the gland; *v. sm.*, the anterior and posterior veins from the gland ending in *v. j.*, the jugular vein; *v. sym.*, the conjoined vagus and sympathetic trunks; *gl. cer. s.*, the superior-cervical ganglion, two branches of which forming a plexus, *a.f.*, over the facial artery are distributed (*n. sym. sm.*) along the two glandular arteries to the anterior and posterior portion of the gland. The arrows indicate the direction taken by the nervous impulses; during reflex stimulations of the gland they ascend to the brain by the lingual and descend by the chorda tympani. (M. Foster.)

of saliva. From these experiments it is evident that the chorda tympani nerve is the principal nerve through which efferent impulses proceed from the centre to excite the secretion of this gland.

The sympathetic fibres appear to act principally as a vaso-constrictor nerve, and to exalt the action of the local vaso-motor centres. The sympathetic is more powerful in this direction than the chorda. There is not sufficient evidence in favour of the belief that the submaxillary ganglion is ever the nerve centre which controls the secretion of the submaxillary gland.

B. On the Parotid Gland.—The nerves which influence secretion in the parotid gland are branches of the facial (lesser superficial petrosal) and of the sympathetic. The former nerve, after passing through the otic ganglion, joins the auriculo-temporal branch of the fifth cerebral nerve, and, with it, is distributed to the gland. The nerves by which the stimulus ordinarily exciting secretion is conveyed to the medulla oblongata, are, as in the case of the submaxillary gland, the fifth, and the glossopharyngeal. The pneumogastric nerves convey a further stimulus to the secretion of saliva, when food has entered the stomach ; the nerve centre is the same as in the case of the submaxillary gland.

Changes in the Gland Cells.—The method by which the salivary cells produce the secretion of saliva appears to be divided into two stages, which differ somewhat according to the class to which the gland belongs, viz., (1) the true salivary, or (2) the mucous type. In the former case, it has been noticed, as has been already described (p. 281), that during the rest which follows an active secretion the lumen of the alveoli becomes smaller, the gland cells larger, and very granular. During secretion the alveoli and their cells become smaller, and the granular appearance in the latter to a considerable extent disappears, and at the end of secretion, the granules are confined to the inner part of the cell nearest to the lumen, which is now quite distinct (fig. 171).

It is supposed from these appearances that the first stage in the act of secretion consists in the protoplasm of the salivary cell taking up from the lymph certain materials from which it manufactures the elements of its own secretion, and which are stored up in the form of granules in the cell during rest, the second stage consisting of the actual discharge of these granules, with or without previous change. The granules are taken to represent the chief substance of the salivary secretion, *i.e.*, the ferment ptyalin. In the case of the submaxillary gland of the dog, at any rate, the sympathetic nerve-fibres appear to have to do with the first stage of the process, and when stimulated the protoplasm is extremely active in manufacturing the granules, whereas the chorda tympani is concerned in the production of the second act, the actual discharge of the materials of secretion, together with a considerable amount of fluid, the latter being an actual secretion by the protoplasm, as it ceases to occur when atropin has been subcutaneously injected.

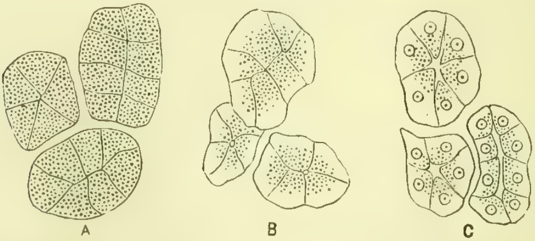

Fig. 171.—*Alveoli of true salivary gland.* A, at rest; B, in the first stage of secretion; C, after prolonged secretion. (Langley.)

In the mucous-secreting gland, the changes in the cells during secretion have been already spoken of (p. 281). They consist in the gradual secretion by the protoplasm of the cell of a substance called *mucigen*, which is converted into *mucin*, and discharged on secretion into the canal of the alveoli. The mucigen is, for the most part, collected into the inner part of the cells during rest, pressing the nucleus and the small portion of the protoplasm which remains, against the limiting membrane of the alveoli.

The process of secretion in the salivary glands is identical with that of glands in general; the cells which line the ultimate branches of the ducts being the agents by which the special constituents of the saliva are formed. The materials which they have incorporated with themselves are almost at once given up again, in the form of a fluid (secretion), which escapes from the ducts of the gland; and the cells, themselves, undergo disintegration,—again to be renewed, in the intervals of the active exercise of their functions. The source whence the cells obtain the materials of their secretion, is the blood, or, to speak more accurately, the plasma, which is filtered off from the circulating blood into the interstices of the glands as of all living textures.

The Pharynx.

That portion of the alimentary canal which intervenes between the mouth and the œsophagus is termed the *Pharynx* (fig. 165). It will suffice here to mention that it is constructed of a series of three muscles with striated fibres (*constrictors*), which are covered by a thin fascia externally, and are lined internally by a strong fascia (pharyngeal aponeurosis), on the inner aspect of which is areolar (submucous) tissue and mucous membrane, continuous with that of the mouth, and, as regards the part concerned in swallowing, is identical with it in general structure. The epithelium of this part of the pharynx, like that of the mouth, is stratified and squamous.

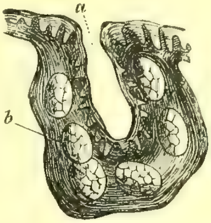

Fig. 172.—*Lingual follicle or crypt.* *a*, involution of mucous membrane with its papillæ; *b*, lymphoid tissue, with several lymphoid sacs. (Frey.)

The pharynx is well supplied with mucous glands (fig. 174).

The Tonsils.—Between the anterior and posterior arches of the soft palate are situated the *Tonsils*, one on each side. A tonsil consists of an elevation of the mucous membrane presenting 12 to 15 orifices, which lead into crypts or recesses, in the walls of which are placed nodules of adenoid or lymphoid tissue (fig. 173). These nodules are enveloped in a less dense adenoid tissue which reaches the mucous surface. The surface is covered with stratified squamous epithelium, and the subepithelial or mucous membrane proper may present rudimentary papillæ formed of adenoid tissue. The tonsil is bounded by a fibrous capsule (fig. 173, *e*). Into the crypts open a number of ducts of mucous glands.

The viscid secretion which exudes from the tonsils serves to lubricate the bolus of food as it passes them in the second part of the act of deglutition.

The Œsophagus or Gullet.

The *Œsophagus* or Gullet (fig. 165), the narrowest portion of the alimentary canal, is a muscular and mucous tube, nine or ten inches in length, which extends from the lower end of the pharynx to the cardiac orifice of the stomach.

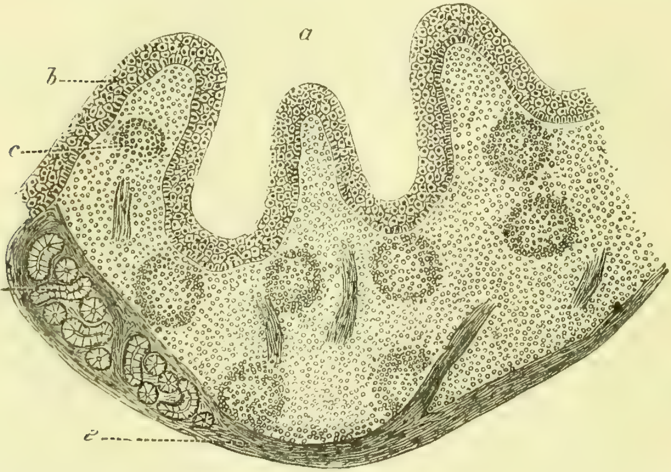

Fig. 173.—*Vertical section through a crypt of the human tonsil.* *a*, entrance to the crypt, which is divided below by the elevation which does not quite reach the surface; *b*, stratified epithelium; *c*, masses of adenoid tissue; *d*, mucous glands cut across; *e*, fibrous capsule. (V. D. Harris.)

Structure.—The œsophagus is made up of three coats—viz., the outer, *muscular;* the middle, *submucous;* and the inner, *mucous.* The *muscular* coat (fig. 175, *g* and *i*) is covered externally by a varying amount of loose fibrous tissue. It is composed of two layers of fibres, the outer being arranged longitudinally, and the inner circularly. At the upper part of the œsophagus this coat is made up principally of striated muscle fibres, as they are continuous with the constrictor muscles of the pharynx; but lower down the unstriated fibres become more and more numerous, and towards the end of the tube form the entire coat. The muscular coat is connected with the mucous coat by a more or less developed layer of areolar tissue, which forms the *submucous* coat (fig. 175, *f*), in which is contained in the lower half or third of the tube many mucous glands, the ducts of which, passing through the mucous membrane (fig. 175, *c*) open on its surface. Separating this coat from the mucous membrane proper is a well-developed layer of longitudinal, unstriated muscle (*d*), called the *muscularis mucosæ*. The mucous membrane is composed of a closely felted meshwork of fine connective tissue, which, towards the surface, is elevated into rudimentary papillæ. It is covered with a stratified epithelium, of which the most superficial layers are squamous. The epithelium is arranged upon a basement membrane.

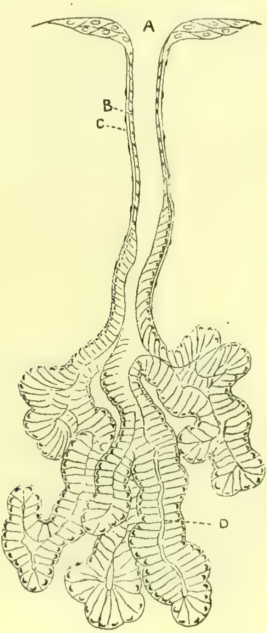

Fig. 174.—*Section of a mucous gland from the tongue.* A, opening of the duct on the free surface; C, basement membrane with nuclei; B, flattened epithelial cells lining duct. The duct divides into several branches, which are convoluted and end blindly, being lined throughout by columnar epithelium. D, lumen of one of the tubuli of the gland. × 90. (Klein and Noble Smith.)

In newly-born children the mucous membrane exhibits, in many parts, the structure of lymphoid tissue (Klein).

Blood- and lymph-vessels, and nerves, are distributed in the walls of the œsophagus. Between the outer and inner layers of the muscular coat, *nerve-ganglia* of Auerbach are also found.

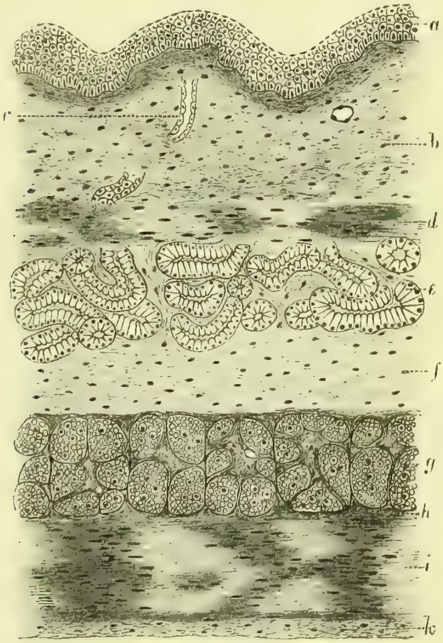

Fig. 175.—*Longitudinal section of œsophagus of a dog towards the lower end.* *a*, stratified epithelium of the mucous membrane; *b*, mucous membrane proper; *c*, duct of mucous gland; *d*, muscularis mucosæ; *e*, mucous glands; *f*, submucous coat; *g*, circular muscular layer; *h*, intermuscular layer, in which is contained the ganglion cells of Auerbach; *i*, longitudinal muscular layer; *k*, outside investment of fibrous tissue. × 100. (V. D. Harris.)

Deglutition or Swallowing.

When properly masticated, the food is transmitted in successive portions to the stomach by the act of *deglutition* or *swallowing*. This, for the purpose of description, may be divided into *three* acts. In the first, particles of food collected to a morsel are made to glide between the surface of the tongue and the palatine arch, till they have passed the anterior arch of the fauces; in the second, the morsel is carried through the pharynx; and in the third, it reaches the stomach through the œsophagus. These three acts follow each other rapidly. (1.) The first act of deglutition may be voluntary, although it is usually performed unconsciously; the morsel of food, when sufficiently masticated, being pressed between the tongue and palate, by the agency of the muscles of the former, in such a manner as to force it back to the entrance of the pharynx. (2.) The second act is the most complicated, because the food must pass by the posterior orifice of the nose and the upper opening of the larynx without touching them. When it has been brought, by the first act, between the anterior arches of the palate, it is moved onwards by the movement of the tongue backwards, and by the muscles of the anterior arches contracting on it and then behind it. The root of the tongue being retracted, and the larynx being raised with the pharynx and carried forwards under the base of the tongue, the epiglottis is pressed over the upper opening of the larynx, and the morsel glides past it; the closure of the glottis being additionally secured by the simultaneous contraction of its own muscles: so that, even when the epiglottis is destroyed, there is little danger of food or drink passing into the larynx so long as its muscles can act freely. At the same time, the raising of the soft palate, so that its posterior edge touches the back part of the pharynx, and the approximation of the sides of the posterior palatine arch, which move quickly inwards like side curtains, close the passage into the upper part of the pharynx and the posterior nares, and form an inclined plane, along the under surface of which the morsel descends; then the pharynx, raised up to receive it, in its turn contracts, and forces it onwards into the œsophagus. (3.) In the third act, in which the food passes through the œsophagus, every part of that tube, as it receives the morsel and is dilated by it, is stimulated to contract: hence an undulatory contraction of the œsophagus, which is easily observable in horses while drinking, proceeds rapidly along the tube. It is only when the morsels swallowed are large, or taken too quickly in succession, that the progressive contraction of the œsophagus is slow, and attended with pain. Division of both pneumogastric nerves paralyses the contractile power of the œsophagus, and food accordingly accumulates in the tube. The second and third parts of the act of deglutition are involuntary.

Nerve Mechanism.—The nerves engaged in the reflex act of deglutition are:—*sensory*, branches of the fifth cerebral supplying the soft palate; glosso-pharyngeal, supplying the tongue and pharynx; the superior laryngeal branch of the vagus, supplying the epiglottis and the glottis; while the *motor* fibres concerned are:—branches of the fifth, supplying part of the digastric and mylo-hyoid muscles, and the muscles of mastication; the facial, supplying the levator palati; the glosso-pharyngeal, supplying the muscles of the pharynx; the vagus, supplying the muscles of the larynx through the inferior laryngeal branch, and the hypoglossal, the muscles of the tongue. The nerve-centre by which the muscles are harmonised in their action, is situate in the medulla oblongata. In the movements of the œsophagus, the ganglia contained in its walls, with the pneumo-gastrics, are the nerve-structures chiefly concerned.

It is important to note that the swallowing both of food and drink is a *muscular* act, and can, therefore, take place in opposition to the force of gravity. Thus, horses and many other animals habitually drink up-hill, and the same feat can be performed by jugglers.

The Stomach.

In man and those Mammalia which are provided with a single stomach, it consists of a dilatation of the alimentary canal placed between and continuous with the œsophagus, which enters its larger or cardiac end on the one hand, and the small intestine, which commences at its narrowed end or pylorus, on the other. It varies in shape and size according to its state of distension.

The *Ruminants* (ox, sheep, deer, &c.) possess very complex stomachs; in most of them four distinct cavities are to be distinguished (fig. 176).

1. The *Paunch* or *Rumen*, a very large cavity which occupies the cardiac end, and into which large quantities of food are in the first instance swallowed with little or no mastication. 2. The *Reticulum*, or *Honeycomb* stomach, so called from the fact that its mucous membrane is disposed in a number of folds enclosing hexagonal cells. 3. The *Psalterium*, or *Manyplies*, in which the mucous membrane is arranged in very prominent longitudinal folds. 4. *Abomasum*, *Reed*, or *Rennet*, narrow and elongated, its mucous membrane being much more highly vascular than that of the other divisions. In the process of rumination small portions of the contents of the rumen and reticulum are successively regurgitated into the mouth, and there thoroughly masticated and insalivated (chewing the cud): they are then again swallowed, being this time directed by a groove (which in the figure is seen running from the lower end of the æsophagus) into the manyplies, and thence into the abomasum. It will thus be seen that the first two stomachs

(paunch and reticulum) have chiefly the mechanical functions of storing and moistening the fodder: the third (manyplies) probably acts as a strainer, only allowing the finely divided portions of food to pass on into the fourth stomach, where the gastric juice is secreted and the process of digestion carried on. The mucous membrane of the first three stomachs is lowly vascular, while that of the fourth is pulpy, glandular, and highly vascular.

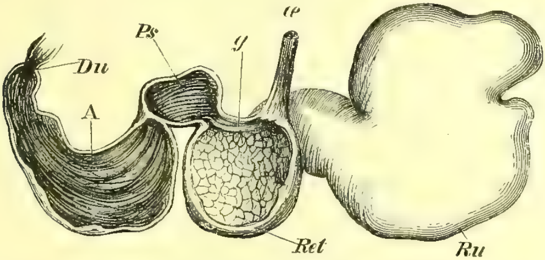

Fig. 176.—*Stomach of sheep.* *œ*, œsophagus; *Ru*, rumen; *Ret*, reticulum; *Ps*, psalterium, or manyplies; *A*, abomasum; *Du*, duodenum; *g*, groove from œsophagus to psalterium. (Huxley.)

In some other animals, as the pig, a similar distinction obtains between the mucous membrane in different parts of the stomach.

In the pig the glands in the cardiac end are few and small, while towards the pylorus they are abundant and large.

A similar division of the stomach into a cardiac (receptive) and a pyloric (digestive) part, foreshadowing the complex stomach of ruminants, is seen in the common rat, in which these two divisions of the stomach are distinguished, not only by the characters of their lining membrane, but also by a well-marked constriction.

In birds the function of mastication is performed by the stomach (gizzard) which in granivorous orders, *e.g.* the common fowl, possesses very powerful muscular walls and a dense horny epithelium.

Structure.—The stomach is composed of four coats, called respectively—an external or (1) *peritoneal*; (2) *muscular*, (3) *submucous*, and (4) *mucous* coat; with blood-vessels, lymphatics, and nerves distributed in and between them.

(1) The *peritoneal* coat has the structure of serous membranes in general (p. 394). (2) The *muscular* coat consists of three separate layers or sets of fibres, which, according to their several directions, are named the longitudinal, circular, and oblique. The *longitudinal* set are the most superficial: they are continuous with the longitudinal fibres of the œsophagus, and spread out in diverging manner over the cardiac end and sides of the stomach. They extend as far as the pylorus, being especially distinct at

the lesser or upper curvature of the stomach, along which they pass in several strong bands. The next set are the *circular* or *transverse* fibres, which more or less completely encircle all parts of the stomach; they are most abundant at the middle and in the pyloric portion of the organ, and form the chief part of the thick projecting ring of the pylorus. These fibres are not simple circles, but form double or figure-of-8 loops, the fibres intersecting very obliquely. The next, and consequently deepest set of fibres, are the *oblique*, continuous with the circular muscular fibres of the œsophagus, and having the same double-looped arrangement that prevails in the preceding layer: they are comparatively few in number, and are placed only at the cardiac orifice and portion of the stomach, over both surfaces of which they are spread, some passing obliquely from left to right, others from right to left, around the cardiac orifice, to which, by their interlacing, they form a kind of sphincter, continuous with that around the lower end of the œsophagus. The muscular fibres of the stomach and of the intestinal canal are *unstriated*, being composed of elongated, spindle-shaped fibre-cells.

(3) and (4) The *mucous membrane* of the stomach, which rests upon a layer of loose cellular membrane, or *submucous tissue*, is smooth, level, soft, and velvety; of a pale pink colour during life, and in the contracted state thrown into numerous, chiefly longitudinal, folds or rugæ, which disappear when the organ is distended.

The basis of the mucous membrane is a fine connective tissue, which approaches closely in structure to adenoid tissue; this tissue supports the tubular glands of which the superficial and chief part of the mucous membrane is composed, and passing up between them assists in binding them together. Here and there are to be found in this coat, immediately underneath the glands, masses of adenoid tissue sufficiently marked to be termed by some lymphoid follicles. The glands are separated from the rest of the mucous membrane by a very fine homogeneous basement membrane.

At the deepest part of the mucous membrane are two layers (circular and longitudinal) of unstriped muscular fibres, called the *muscularis mucosæ*, which separate the mucous membrane from the scanty submucous tissue.

When examined with a lens, the internal or free surface of the stomach presents a peculiar honeycomb appearance, produced by shallow polygonal depressions, the diameter of which varies generally from $\frac{1}{200}$th to $\frac{1}{350}$th of an inch; but near the pylorus is as much as $\frac{1}{100}$th of an inch. They are separated by slightly elevated ridges, which sometimes, especially in certain morbid states of the stomach, bear minute, narrow vascular processes, which look like villi, and have given rise to the erroneous supposition that the stomach has absorbing villi, like those of the small intestines. In the bottom of these little pits, and to some extent between them, minute openings are visible, which are the orifices of the ducts of perpendicularly arranged tubular glands (fig. 177), imbedded side by side in sets or bundles, on the surface of the mucous membrane, and composing nearly the whole structure.

Gastric Glands.—Of these there are two varieties, (*a*) Peptic, (*b*) Pyloric or Mucous.

(*a*) *Peptic* glands are found throughout the whole of the stomach except at the pylorus. They are arranged in groups of four or five, which are separated by a fine connective tissue. Two or three tubes often open into one duct, which forms about a third of the whole length of the tube and opens on the surface. The ducts are lined with columnar epithelium. Of the gland tube proper, *i.e.*, the part of the gland below the duct, the upper third is the *neck* and the rest the *body*. The neck is narrower than the body, and is lined with granular cubical cells which are continuous with the columnar cells of the duct. Between these cells and the membrana propria of the tubes, are large oval or spherical cells, opaque or granular in appearance, with clear oval nuclei, bulging out the membrana propria; these cells are called *peptic or parietal cells*. They do not form a continuous layer. The body, which is broader than the neck and terminates in a blind extremity or *fundus* near the muscularis mucosæ, is lined by cells continuous with the cubical or central cells of the neck, but longer, more columnar and more transparent. In this part are a few parietal cells of the same kind as in the neck (fig. 177).

As the pylorus is approached the gland ducts become longer, and the tube proper becomes shorter, and occasionally branched at the fundus.

(*b*) *Pyloric Glands.*—These glands (fig. 179) have much longer ducts than the peptic glands. Into each duct two or three tubes open by very short and narrow necks, and the body of each tube is branched, wavy, and convoluted. The lumen is very large.

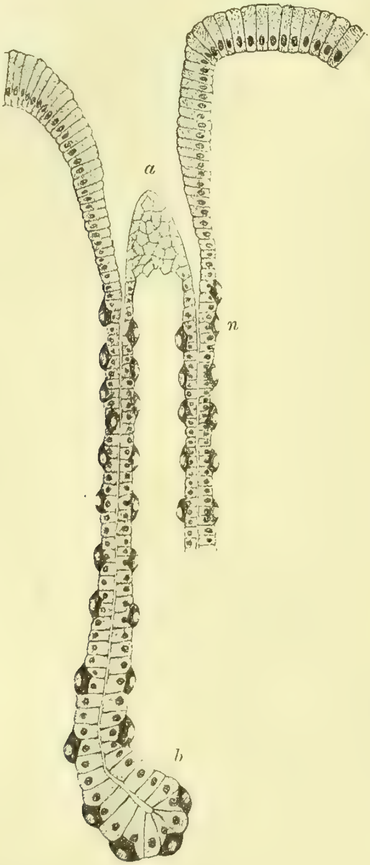

Fig. 177.—*From a vertical section through the mucous membrane of the cardiac end of stomach.* Two peptic glands are shown with a duct common to both, one gland only in part. *a*, duct with columnar epithelium becoming shorter as the cells are traced downward; *n*, neck of gland tubes, with central and parietal or so-called peptic cells; *b*, fundus with curved cæcal extremity—the parietal cells are not so numerous here. × 400. (Klein and Noble Smith.)

The ducts are lined with columnar epithelium, and the neck and body with shorter and more granular cubical cells, which correspond with the central cells of the peptic glands. During secretion the cells become, as in the case of the peptic glands, larger and the granules restricted to the inner zone of the cell. As they approach the duodenum the pyloric glands become larger, more convoluted and more deeply situated. They are directly continuous with Brunner's glands in the duodenum. (Watney.)

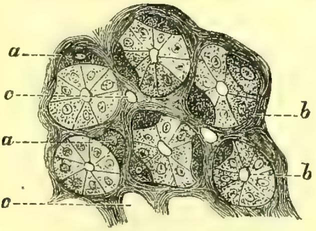

Fig. 178.—*Transverse section through lower part of peptic glands of a cat.* a, peptic cells; b, small spheroidal or cubical cells; c, transverse section of capillaries. (Frey.)

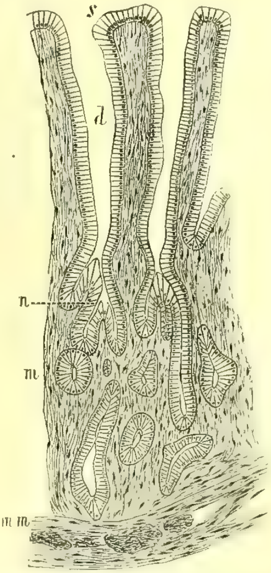

Fig. 179.—*Section showing the pyloric glands.* s, free surface; d, ducts of pyloric glands; n, neck of same; m, the gland alveoli; mm, muscularis mucosæ. (Klein and Noble Smith.)

Changes in the gland cells during secretion.—The chief or cubical cells of the peptic glands, and the corresponding cells of the pyloric glands during the early stage of digestion, if hardened in alcohol, appear swollen and granular, and stain readily. At a later stage the cells become smaller, but more granular and stain even more readily. The parietal cells swell up, but are otherwise not altered during digestion. The granules, however, in the alcohol-hardened specimen, are believed not to exist in the living cells, but to have been precipitated by the hardening re-agent; for if examined during life they appear to be confined to the inner zone of the cells, and the outer zone is free from granules, whereas during rest the cell is granular throughout. These granules are thought to be pepsin, or the substance from which pepsin is formed, *pepsinogen*, which is during rest stored chiefly in the inner zone of the cells and discharged into the lumen of the tube during secretion. (Langley.)

Lymphatics.—Lymphatic vessels surround the gland tubes to a greater or less extent. Towards the fundus of the peptic glands are found masses of lymphoid tissue, which may appear as distinct follicles, somewhat like the solitary glands of the small intestine.

Blood-vessels.—The blood-vessels of the stomach, which first break up in the submucous tissue, send branches upward between the closely packed glandular tubes, anastomosing around them by means of a fine capillary network, with oblong meshes. Continuous with this deeper plexus, or prolonged upwards from it, so to speak, is a more superficial network of larger capillaries, which branch densely around the orifices of the tubes, and form the framework on which are moulded the small elevated ridges of mucous membrane bounding the minute, polygonal pits before referred to. From this *superficial* network the veins chiefly take their origin. Thence passing down between the tubes, with no very free connection with the deeper *inter-tubular* capillary plexus, they open finally into the venous network in the submucous tissue.

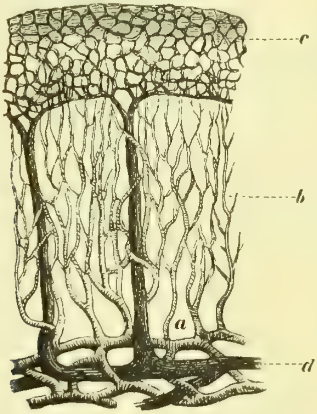

Fig. 180.—*Plan of the blood-vessels of the stomach*, as they would be seen in a vertical section. *a*, arteries, passing up from the vessels of submucous coat; *b*, capillaries branching between and around the tubes; *c*, superficial plexus of capillaries occupying the ridges of the mucous membrane; *d*, vein formed by the union of veins which, having collected the blood of the superficial capillary plexus, are seen passing down between the tubes. (Brinton.)

Nerves.—The nerves of the stomach are derived from the pneumogastric and sympathetic, and form a plexus in the submucous and muscular coats, containing many ganglia (Remak, Meissner).

Digestion in the Stomach.

Gastric Juice.—The functions of the stomach are to secrete a digestive fluid (gastric juice), to the action of which the food is next subjected after it has entered the cavity of the stomach from the œsophagus; to thoroughly incorporate the fluid with the food by means of its muscular movements; and to absorb such substances as are capable of absorption. While the stomach contains no food, and is inactive, no gastric fluid is secreted; and mucus, which is either neutral or slightly alkaline, covers its surface. But immediately on the introduction of food or other substance the mucous membrane, previously quite pale, becomes slightly turgid and reddened with the influx of a larger quantity of blood; the gastric glands commence secreting actively, and an acid fluid is poured out in minute drops, which gradually run together and flow down the walls of the stomach, or soak into the substances within it.

Chemical Composition of Gastric Juice.—The first accurate analysis of gastric juice was made by Prout: but it does not appear to have been collected in any large quantity, or pure and separate from food, until the time when Beaumont was enabled, by a fortunate circumstance, to obtain it from the stomach of a man named St. Martin, in whom there existed, as the result of a gunshot wound, an opening leading directly into the stomach, near the upper extremity of the great curvature, and three inches from the cardiac orifice. The introduction of any mechanical irritant, such as the bulb of a thermometer, into the stomach, excited at once the secretion of gastric fluid. This was drawn off, and was often obtained to the extent of nearly an ounce. The introduction of alimentary substances caused a much more rapid and abundant secretion than did other mechanical irritants. No increase of temperature could be detected during the most active secretion; the thermometer introduced into the stomach always stood at 100° F. (37·8° C.) except during muscular exertion, when the temperature of the stomach, like that of other parts of the body, rose one or two degrees higher.

The chemical composition of human gastric juice has been also investigated by Schmidt. The fluid in this case was obtained by means of an accidental gastric fistula, which existed for several years below the left mammary region of a patient between the cartilages of the ninth and tenth ribs. The mucous membrane was excited to action by the introduction of some hard matter, such as dry peas, and the secretion was removed by means of an elastic tube. The fluid thus obtained was found to be acid, limpid, odourless, with a mawkish taste—with a specific gravity of 1002, or a little more. It contained a few cells, seen with the microscope, and some fine granular matter. The analysis of the fluid obtained in this is given below. The gastric juice of dogs and other animals obtained by the introduction into the stomach of a clean sponge through an artificially made gastric fistula, shows a decided difference in composition, but possibly this is due, at least in part, to admixture with food.

Chemical Composition of Gastric Juice.

	Dog's.	Human.
Water	971·17	994·4
Solids	28·82	5·39
Solids—		
Ferment—Pepsin	17·5	3·19
Hydrochloric acid (free)	2·7	·2
Salts—		
Calcium, sodium, and potassium, chlorides; and calcium, magnesium, and iron, phosphates	8·57	2·19

The *quantity* of gastric juice secreted daily has been variously estimated; but the average for a healthy adult may be assumed to range from ten to twenty pints in the twenty-four hours. The acidity of the fluid is due to free *hydrochloric* acid, although other acids, *e.g.*, *lactic*, *acetic*, *butyric*, are not unfrequently to be found therein as products of gastric digestion. The amount of hydrochloric acid varies from 2 to ·2 per 1000 parts. In healthy gastric juice the amount of free acid may be as much as ·2 per cent.

As regards the formation of pepsin and acid, the former is produced by the central or chief cells of the peptic glands, and also most likely by the similar cells in the pyloric glands; the acid is chiefly found at the surface of the mucous membrane, but is in all probability formed by the secreting action of the parietal cells of the peptic glands, as no acid is formed by the pyloric glands in which this variety of cell is absent.

The ferment *Pepsin* (p. 305) can be procured by digesting portions of the mucous membrane of the stomach in cold water, after they have been macerated for some time in water at a temperature 80°—100° F. (27·°—37·8° C.). The warm water dissolves various substances as well as some of the pepsin, but the cold water takes up little else than pepsin, which is contained in a greyish-brown viscid fluid, on evaporating the cold solution. The addition of alcohol throws down the pepsin in greyish-white flocculi. Glycerine also has the property of dissolving out the ferment; and if the mucous membrane be finely minced and the moisture removed by absolute alcohol, a powerful extract may be obtained by throwing into glycerine.

Functions.—The digestive power of the gastric juice depends on the pepsin and acid contained in it, both of which are, under ordinary circumstances, necessary for the process.

The general effect of digestion in the stomach is the conversion of the food into *chyme*, a substance of various composition according to the nature of the food, yet always presenting a characteristic thick, pultaceous, grumous consistence, with the undigested portions of the food mixed in a more fluid substance, and a strong, disagreeable acid odour and taste.

The chief function of the gastric juice is to *convert proteids into peptones.* This action may be shown by adding a little gastric juice (natural or artificial) to some diluted egg-albumin, and keeping the mixture at a temperature of about 100° F. (37·8° C.); it is soon found that the albumin cannot be precipitated on boiling, but that if the solution be neutralised with an alkali, a precipitate of acid-albumin is thrown down. After a while the proportion of acid-albumin gradually diminishes, so that at last scarcely any precipitate results on neutralization, and finally it is found that all the albumin has been changed into another proteid substance which is not precipitated on boiling or on neutralization. This is called *peptone.*

Characteristics of Peptones.—Peptones have certain characteristics which distinguish them from other proteids. 1. They are *diffusible*, *i.e.*, they possess the property of passing through animal membranes. 2. They cannot be precipitated by heat, nitric, or acetic acid, or potassium ferrocyanide and acetic acid. They are, however, thrown down by tannic acid, by mercuric chloride and by picric acid. 3. They are very soluble in water and in neutral saline solutions.

In their diffusibility peptones differ remarkably from egg-albumin, and on this diffusibility depends one of their chief uses. Egg-albumin as such, even in a state of solution, would be of little service as food, inasmuch as its indiffusibility would effectually prevent its passing by absorption into the blood-vessels of the stomach and intestinal canal. Changed, however, by the action of the gastric juice into peptones, albuminous matters *diffuse* readily, and are thus quickly absorbed.

After entering the blood the peptones are very soon again modified, so as to re-assume the chemical characters of albumin, a change as necessary for preventing their diffusing out of the blood-vessels, as the previous change was for enabling them to pass in. This is effected, probably, in great part by the agency of the liver.

Products of Gastric Digestion.—The chief product of gastric digestion is undoubtedly peptone. We have seen, however, in the above experiment that there is a by-product, and this is almost identical with syntonin or acid albumin. This body is probably not exactly identical, however, with syntonin, and its old name of *parapeptone* had better be retained. The conversion of native albumin into acid albumin may be effected by the hydrochloric acid alone, but the further action is undoubtedly due to the ferment and the acid together, as although under high pressure any acid solution may, it is said, if strong enough, produce the entire conversion into peptone, under the condition of digestion in the stomach this would be quite impossible; and, on the other hand, pepsin will not act without the presence of acid. The production of two forms of peptone is usually recognised, called respectively *anti*-peptone and *hemi*-peptone. Their differences in chemical properties have not yet been made out, but they are distinguished by this remarkable fact, that the pancreatic juice, while possessing no action over the former, is able to convert the latter into leucin and tyrosin. Pepsin acts the part of a hydrolytic ferment (proteolytic), and appears to cause hydration of albumin, peptone being a highly hydrated form of albumin.

Circumstances favouring Gastric Digestion. 1.—A temperature of about 100° F. (37·8° C.); at 32° F. (0° C.) it is delayed, and by boiling is altogether stopped. 2. An acid medium is necessary. Hydrochloric is the best acid for the purpose. Excess of acid or neutralization stops the process. 3. The removal of the products of digestion. Excess of peptone delays the action.

Action of the Gastric Juice on Bodies other than Proteids.—All proteids are converted by the gastric juice into peptones, and, therefore, whether they be taken into the body in meat, eggs, milk, bread, or other foods, the resultant still is peptone.

Milk is curdled, the casein being precipitated, and then dissolved. The curdling is due to a special ferment of the gastric juice (curdling ferment), and is not due to the action of the free acid only. The effect of rennet, which is a decoction of the fourth stomach of a calf in brine, has long been known, as it is used extensively to cause precipitation of casein in cheese manufacture.

The ferment which produces this curdling action is distinct from pepsin.

Gelatin is dissolved and changed into peptone, as are also *chondrin* and *elastin;* but *mucin*, and the *horny tissues*, keratin generally are unaffected.

On the *amylaceous* articles of food, and upon pure *oleaginous* principles the gastric juice has no action. In the case of adipose tissue, its effect is to dissolve the areolar tissue, albuminous cell-walls, etc., which enter into its composition, by which means the fat is able to mingle more uniformly with the other constituents of the *chyme.*

The gastric fluid acts as a general solvent for some of the *saline* constituents of the food, as, for example, particles of common salt, which may happen to have escaped solution in the saliva; while its acid may enable it to dissolve some other salts which are insoluble in the latter or in water. It also dissolves cane *sugar*, and by the aid of its mucus causes its conversion in part into grape sugar.

The action of the gastric juice in preventing and checking putrefaction has been often directly demonstrated. Indeed, that the secretions which the food meets with in the alimentary canal are *antiseptic* in their action, is what might be anticipated, not only from the proneness to decomposition of organic matters, such as those used as food, especially under the influence of warmth and moisture, but also from the well-known fact that decomposing flesh (*e.g.*, high game) may be eaten with impunity, while it would certainly cause disease were it allowed to enter the blood by any other route than that formed by the organs of digestion.

Time occupied in Gastric Digestion.—Under ordinary conditions, from three to four hours may be taken as the average time occupied by the digestion of a meal in the stomach. But many circumstances will modify the rate of gastric digestion. The chief are: the *nature* of the food taken and its *quantity* (the stomach should be fairly filled—not distended); the time that has elapsed since the last meal, which should be at least enough for the stomach to be quite clear of food; the amount of exercise previous and subsequent to a meal (gentle exercise being favourable, over-exertion injurious to digestion); the state of mind (tranquillity of temper being essential, in most cases, to a quick and due digestion); the bodily health; and some others.

Movements of the Stomach.—The gastric fluid is assisted in accomplishing its share in digestion by the movements of the stomach. In granivorous birds, for example, the contraction of the strong muscular gizzard affords a necessary aid to digestion, by grinding and triturating the hard seeds which constitute part of the food. But in the stomachs of man and other Mammalia the motions of the muscular coat are too feeble to exercise any such mechanical force on the food; neither are they needed, for mastication has already done the mechanical work of a gizzard; and experiments have demonstrated that substances enclosed in perforated tubes, and consequently protected from mechanical influence, are yet digested.

The normal actions of the muscular fibres of the human stomach appear to have a three-fold purpose; (1) to adapt the stomach to the quantity of food in it, so that its walls may be in contact with the food on all sides, and, at the same time, may exercise a certain amount of compression upon it; (2) to keep the orifices of the stomach closed until the food is digested; and (3) to perform certain peristaltic movements, whereby the food, as it becomes chymified, is gradually propelled towards, and ultimately through, the pylorus. In accomplishing this latter end, the movements without doubt materially contribute towards effecting a thorough intermingling of the food and the gastric fluid.

When digestion is not going on, the stomach is uniformly contracted, its orifices not more firmly than the rest of its walls; but, if examined shortly after the introduction of food, it is found closely encircling its contents, and its orifices are firmly closed like sphincters. The cardiac orifice, every time food is swallowed, opens to admit its passage to the stomach, and immediately again closes. The pyloric orifice, during the first part of gastric digestion, is usually so completely closed, that even when the stomach is separated from the intestines, none of its contents escape. But towards the termination of the digestive process, the pylorus seems to offer less resistance to the passage of substances from the stomach; first it yields to allow the successively digested portions to go through it; and then it allows the transit of even undigested substances. It appears that food, so soon as it enters the stomach, is subjected to a kind of peristaltic action of the muscular coat, whereby the digested portions are gradually moved towards the pylorus. The movements were observed to increase in rapidity as the process of chymification advanced, and were continued until it was completed.

The contraction of the fibres situated towards the pyloric end of the stomach seems to be more energetic and more decidedly peristaltic than those of the cardiac portion. Thus, it was found in the case of St. Martin, that when the bulb of the thermometer was placed about three inches from the pylorus, through the gastric fistula, it was tightly embraced from time to time, and drawn towards the pyloric orifice for a distance of three or four inches. The object of this movement appears to be, as just said, to carry the food towards the pylorus as fast as it is formed into chyme, and to propel the chyme into the duodenum; the undigested portions of food being kept back until they are also reduced into chyme, or until all that is digestible has passed out. The action of these fibres is often seen in the contracted state of the pyloric portion of the stomach after death, when it alone is contracted and firm, while the cardiac portion forms a dilated sac. Sometimes, by a predominant action of strong circular fibres placed between the cardia and pylorus, the two portions, or ends as they are called, of the stomach, are partially separated from each other by a kind of hourglass contraction. By means of the peristaltic action of the muscular coats of the stomach, not merely is chymified food gradually propelled through the pylorus, but a kind of double current is continually kept up among the contents of the stomach, the circumferential parts of the mass being gradually moved onward towards the pylorus by the contraction of the muscular fibres, while the central portions are propelled in the opposite direction, namely, towards the cardiac orifice; in this way is kept up a constant circulation of the contents of the viscus, highly conducive to their free mixture with the gastric fluid and to their ready digestion.

Vomiting.—The expulsion of the contents of the stomach in vomiting, like that of mucous or other matter from the lungs in *coughing*, is preceded by an inspiration; the glottis is then closed, and immediately afterwards the abdominal muscles strongly act; but here occurs the difference in the two actions. Instead of the vocal cords yielding to the action of the abdominal muscles, they remain tightly closed. Thus the diaphragm being unable to go up, forms an unyielding surface against which the stomach can be pressed. In this way, as well as by its own contraction, it is *fixed*, to use a technical phrase. At the same time the *cardiac* sphincter-muscle being relaxed, and the orifice which it naturally guards being actively dilated, while the *pylorus* is closed, and the stomach itself also contracting, the action of the abdominal muscles, by these means assisted, expels the contents of the organ through the œsophagus, pharynx, and mouth. The reversed peristaltic action of the œsophagus probably increases the effect.

It has been frequently stated that the stomach itself is quite passive during vomiting, and that the expulsion of its contents is effected solely by the pressure exerted upon it when the capacity of the abdomen is diminished by the contraction of the diaphragm, and subsequently of the abdominal muscles. The experiments and observations, however, which are supposed to confirm this statement, only show that the contraction of the abdominal muscles alone is sufficient to expel matters from an unresisting bag through the œsophagus; and that, under very abnormal circumstances, the stomach, by itself, cannot expel its contents. They by no means show that in ordinary vomiting the stomach is passive; and, on the other hand, there are good reasons for believing the contrary.

It is true that facts are wanting to demonstrate with certainty this action of the stomach in vomiting; but some of the cases of fistulous opening into the organ appear to support the belief that it does take place; and the analogy of the case of the stomach with that of the other hollow viscera, as the rectum and bladder, may be also cited in confirmation.

The *muscles* concerned in the act of vomiting, are chiefly and primarily *those of the abdomen;* the *diaphragm* also acts, but usually not as the muscles of the abdominal walls do. They contract and compress the stomach more and more towards the diaphragm; and the diaphragm (which is usually drawn down in the deep inspiration that precedes each act of vomiting) is fixed, and presents an unyielding surface against which the stomach may be pressed. The diaphragm is, therefore, as a rule passive, during the actual expulsion of the contents of the stomach. But there are grounds for believing that sometimes this muscle actively contracts, so that the stomach is, so to speak, squeezed between the descending diaphragm and the retracting abdominal walls.

Some persons possess the power of *vomiting at will*, without applying any undue irritation to the stomach, but simply by a voluntary effort. It seems also, that this power may be acquired by those who do not naturally possess it, and by continual practice may become a habit. There are cases also of rare occurrence in which persons habitually swallow their food hastily, and nearly unmasticated, and then at their leisure regurgitate it, piece by piece, into their mouth, remasticate, and again swallow it, like members of the ruminant order of Mammalia.

The various *nerve-actions* concerned in vomiting are governed by a nerve-centre situate in the medulla oblongata.

The sensory nerves are the fifth, glosso-pharyngeal and vagus principally; but, as well, vomiting may occur from stimulation of sensory nerves from many organs, *e.g.*, kidney, testicle, &c. The centre may also be stimulated by impressions from the cerebrum and cerebellum, so called *central* vomiting occurring in disease of those parts. The efferent impulses are carried by the phrenics and the spinal nerves.

Influence of the Nervous System on Gastric Digestion.—The normal movements of the stomach during gastric digestion are directly connected with the plexus of nerves and ganglia contained in its walls, the presence of food acting as a stimulus which is conveyed to the ganglia and reflected to the muscular fibres. The stomach is, however, also directly connected with the higher nerve-centres by means of branches of the vagus and solar plexus of the sympathetic. The vaso-motor fibres of the latter are derived, probably, from the splanchnic nerves.

The exact function of the vagi in connection with the movements of the stomach is not certainly known. Irritation of the vagi produces contraction of the stomach, if digestion is proceeding; while, on the other hand, peristaltic action is retarded or stopped, when these nerves are divided.

Bernard, watching the act of gastric digestion in dogs which had fistulous openings into their stomachs, saw that on the instant of dividing their vagic nerves, the process of digestion was stopped, and the mucous membrane of the stomach, previously turgid with blood, became pale, and ceased to secrete. These facts may be explained by the theory that the vagi are the media by which, during digestion, an *inhibitory* impulse is conducted to the vaso-motor centre in the medulla; such impulse being reflected along the splanchnic nerves to the blood-vessels of the stomach, and causing their dilatation (Rutherford). From other experiments it may be gathered, that although division of both vagi always temporarily suspends the secretion of gastric fluid, and so arrests the process of digestion, being occasionally followed by death from inanition; yet the digestive powers of the stomach may be completely restored after the operation, and the formation of chyme and the nutrition of the animal may be carried on almost as perfectly as in health. This would indicate the existence of a special local nervous mechanism which controls the secretion.

Bernard found that galvanic stimulus of these nerves excited an active secretion of the fluid, while a like stimulus applied to the sympathetic nerves issuing from the semilunar ganglia, caused a diminution and even complete arrest of the secretion.

The influence of the higher nerve-centres on gastric digestion, as in the case of mental emotion, is too well known to need more than a reference.

Digestion of the Stomach after Death.—If an animal die during the process of gastric digestion, and when, therefore, a quantity of gastric juice is present in the interior of the stomach, the walls of this organ itself are frequently themselves acted on by their own secretion, and to such an extent, that a perforation of considerable size may be produced, and the contents of the stomach may in part escape into the cavity of the abdomen. This phenomenon is not unfrequently observed in *post-mortem* examinations of the human body. If a rabbit be killed during a period of digestion, and afterwards exposed to artificial warmth to prevent its temperature from falling, not only the stomach, but many of the surrounding parts will be found to have been dissolved (Pavy).

From these facts, it becomes an interesting question why, during life, the stomach is free from liability to injury from a secretion, which, after death, is capable of such destructive effects?

It is only necessary to refer to the idea of Bernard, that the living stomach finds protection from its secretion in the presence of epithelium and mucus, which are constantly renewed in the same degree that they are constantly dissolved, in order to remark that although the gastric mucus is probably protective, this theory, so far as the *epithelium* is concerned, has been disproved by experiments of Pavy's, in which the mucous membrane of the stomachs of dogs was dissected off for a small space, and, on killing the animals some days afterwards, no sign of digestion of the stomach was visible. "Upon one occasion, after removing the mucous membrane, and exposing the muscular fibres over a space of about an inch and a half in diameter, the animal was allowed to live for ten days. It ate food every day, and seemed scarcely affected by the operation. Life was destroyed whilst digestion was being carried on, and the lesion in the stomach was found very nearly repaired: new matter had been deposited in the place of what had been removed, and the denuded spot had contracted to much less than its original dimensions."

Pavy believes that the natural alkalinity of the blood, which circulates so freely during life in the walls of the stomach, is sufficient to neutralize the acidity of the gastric juice; and as may be gathered from what has been previously said, the neutralization of the acidity of the gastric secretion is quite sufficient to destroy its digestive powers; but the experiments adduced in favour of this theory are open to many objections, and afford only a negative support to the conclusions they are intended to prove. Again, the pancreatic secretion acts best on proteids in an *alkaline* medium; but it has no digestive action on the living intestine. It must be confessed that no entirely satisfactory theory has been yet stated.

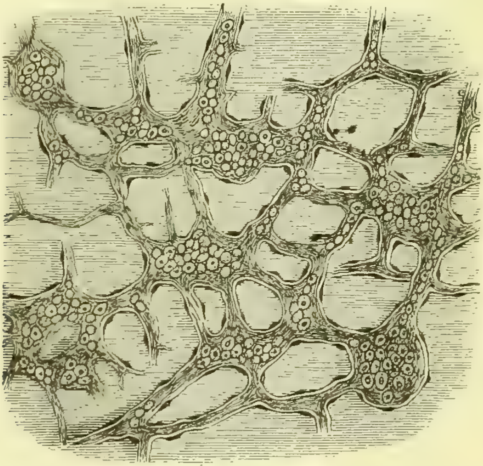

Fig. 181.—*Auerbach's nerve-plexus in small intestine.* The plexus consists of fibrillated substance, and is made up of trabeculæ of various thicknesses. Nucleus-like elements and ganglion-cells are imbedded in the plexus, the whole of which is enclosed in a nucleated sheath. (Klein.)

The Intestines.

The Intestinal Canal is divided into two chief portions, named from their differences in diameter, the (I.) *small* and (II.) *large* intestine (fig. 165). These are continuous with each other, and communicate by means of an opening guarded by a valve, the *ileo-cæcal* valve, which allows the passage of the products of digestion from the small into the large bowel, but not, under ordinary circumstances, in the opposite direction.

I. The Small Intestine.—The Small Intestine, the average length of which in an adult is about twenty feet, has been divided, for convenience of description, into three portions, viz., the *duodenum*, which extends for eight or ten inches beyond the pylorus; the *jejunum*, which forms two-fifths, and the *ileum*, which forms three-fifths of the rest of the canal.

Structure.—The small intestine, like the stomach, is constructed of four principal coats, viz., the serous, muscular, submucous, and mucous.

(1.) The *serous* coat, formed by the visceral layer of the peritoneum, and has the structure of serous membranes in general.

(2.) The *muscular* coats consist of an internal circular and an external longitudinal layer: the former is usually considerably the thicker. Both alike consist of bundles of unstriped muscular tissue supported by connective tissue. They are well provided with lymphatic vessels, which form a set distinct from those of the mucous membrane.

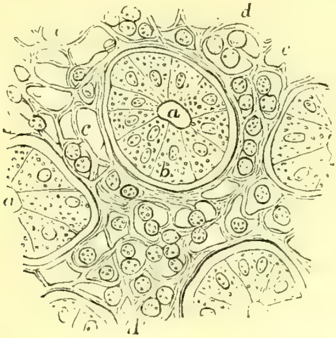

Fig. 182.—*Horizontal section of a small fragment of the mucous membrane*, including one entire crypt of Lieberkühn and parts of several others: *a*, cavity of the tubular glands or crypts; *b*, one of the lining epithelial cells; *c*, the lymphoid or retiform spaces, of which some are empty, and others occupied by lymph cells, as at *d*.

Between the two muscular coats is a nerve-plexus (Auerbach's plexus, plexos myentericus) (fig. 181) similar in structure to Meissner's (in the submucous tissue), but with more numerous ganglia. This plexus regulates the peristaltic movements of the muscular coats of the intestines.

(3.) Between the mucous and muscular coats, is the *submucous* coat, which consists of connective tissue, in which numerous blood-vessels and lymphatics ramify. A fine plexus, consisting mainly of non-medullated nerve-fibres, "Meissner's plexus," with ganglion cells at its nodes, occurs in the submucous tissue from the stomach to the anus. From the position of this plexus and the distribution of its branches, it seems highly probable that it is the local centre for regulating the calibre of the blood-vessels supplying the intestinal mucous membrane, and presiding over the processes of secretion and absorption.

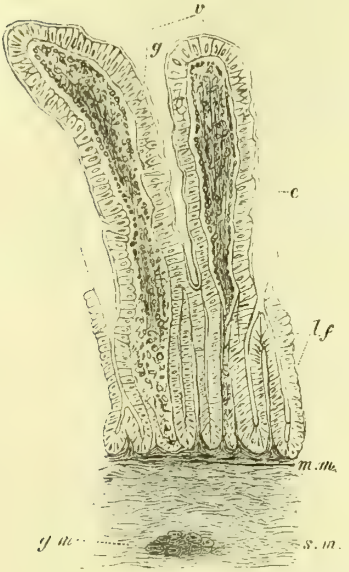

Fig. 183.—*Vertical section through portion of small intestine of dog. v*, two villi showing *e*, epithelium; *g*, goblet cells. The free surface is seen to be formed by the "striated basilar border," while inside the villus the adenoid tissue and unstriped muscle-cells are seen; *lf*, Lieberkühn's follicles; *m m*, muscularis mucosæ, sending up fibres between the follicles into the villi; *sm*, submucous tissue; containing (*gm*), ganglion cells of Meissner's plexus. (Schofield.)

(4.) The *mucous membrane* is the most important coat in relation to the function of digestion. The following structures, which enter into its composition, may now be successively described;—the *valvulæ conniventes;* the *villi;* and the *glands.* The general structure of the mucous membrane of the intestines resembles that of the stomach (p. 298), and, like it, is lined on its inner surface by columnar epithelium. Adenoid tissue (fig. 182, *c* and *d*) enters largely into its construction; and on its deep surface is the *muscularis mucosæ* (*m m*, fig. 183), the fibres of which are arranged in two layers: the outer longitudinal and the inner circular.

Valvulæ Conniventes.—The *valvulæ conniventes* (fig. 184) commence in the duodenum, about one or two inches beyond the pylorus, and becoming larger and more numerous immediately beyond the entrance of the bile duct, continue thickly arranged and well developed throughout the jejunum; then, gradually diminishing in size and number, they cease near the middle of the ileum. They are formed by a doubling inwards of the mucous membrane; the crescentic, nearly circular, folds thus formed being arranged transversely to the axis of the intestine, and each individual fold seldom extending around more than $\frac{1}{2}$ or $\frac{2}{3}$ of the bowel's circumference. Unlike the rugæ in the œsophagus and stomach, they do not disappear on distension of the canal. Only an imperfect notion of their natural position and function can be obtained by looking at them after the intestine has been laid open in the usual manner. To understand them aright, a piece of gut should be distended either with air or alcohol, and not opened until the tissues have become hardened. On then making a section it will be seen that, instead of disappearing, they stand out at right angles to the general surface of the mucous membrane (fig. 184). Their functions are probably less—Besides (1) offering a largely increased surface for secretion and absorption, they probably (2) prevent the too rapid passage of the very liquid products of gastric digestion, immediately after their escape from the stomach, and (3), by their projection, and consequent interference with an uniform and untroubled current of the intestinal contents, probably assist in the more perfect mingling of the latter with the secretions poured out to act on them.

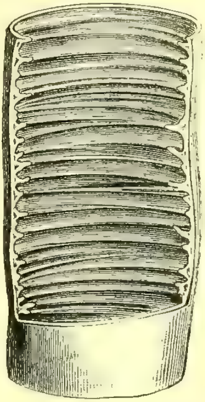

Fig. 184.—*Piece of small intestine (previously distended and hardened by alcohol)* laid open to show the normal position of the valvulæ conniventes.

Glands of the Small Intestine.—The glands are of three principal kinds:—viz., those of (1) Lieberkühn, (2) Brunner, and (3) Peyer.

(1.) The *glands* or *crypts of Lieberkühn* are simple tubular depressions of the intestinal mucous membrane, thickly distributed over the whole surface both of the large and small intestines. In the small intestine they are visible only with the aid of a lens; and their orifices appear as minute dots scattered between the villi. They are larger in the large intestine, and increase in size the nearer they approach the anal end of the intestinal tube; and in the rectum their orifices may be visible to the naked eye. In length they vary from $\frac{1}{30}$ to $\frac{1}{10}$ of a line. Each tubule (fig. 186) is constructed of the same essential parts as the intestinal mucous membrane, viz., a fine *membrana propria*, or basement membrane, a layer of cylindrical epithelium lining it, and capillary blood-vessels covering its exterior, the free surface of the columnar cells presenting an appearance precisely similar to the "striated basilar border" which covers the villi. Their contents appear to vary, even in health; the varieties being dependent, probably, on the period of time in relation to digestion at which they are examined.

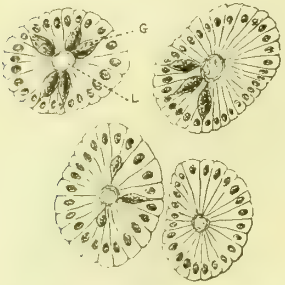

Fig. 185.—*Transverse section through four crypts of Lieberkühn* from the large intestine of the pig. They are lined by columnar epithelial cells, the nuclei being placed in the outer part of the cells. The divisions between the cells are seen as lines radiating from L, the lumen of the crypt; G, epithelial cells, which have become transformed into goblet cells. × 350. (Klein and Noble Smith.)

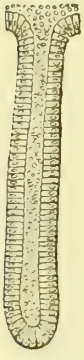

Fig. 186.—*A gland of Lieberkühn in longitudinal section.* (Brinton.)

Among the columnar cells of Lieberkühn's follicles, goblet-cells frequently occur (fig. 185).

(2.) *Brunner's glands* (fig. 188) are confined to the duodenum; they are most abundant and thickly set at the commencement of this portion of the intestine, diminishing gradually as the duodenum advances. They are situated beneath the mucous membrane, and imbedded in the submucous tissue, each gland is a branched and convoluted tube, lined with columnar epithelium. As before said in structure they are very similar to the pyloric glands of the stomach, and their epithelium undergoes a similar change during secretion; but they are more branched and convoluted and their ducts are longer. (Watney.) The duct of each gland passes through the muscularis mucosæ, and opens on the surface of the mucous membrane.

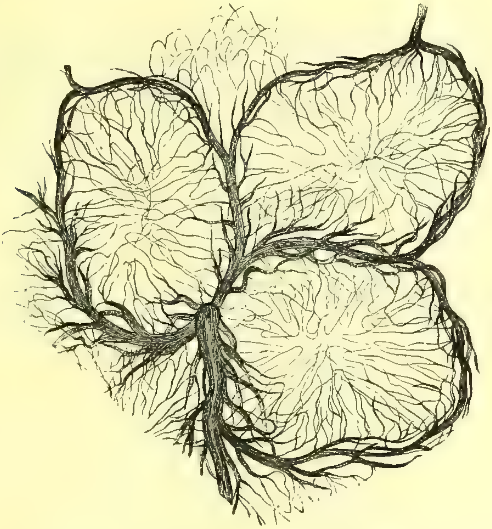

Fig. 187.—*Transverse section of injected Peyer's glands* (from Kölliker). The drawing was taken from a preparation made by Frey: it represents the fine capillary-looped network spreading from the surrounding blood-vessels into the interior of three of Peyer's capsules from the intestine of the rabbit.

(3.) The *glands of Peyer* occur chiefly but not exclusively in the *small* intestine. They are found in greatest abundance in the lower part of the ileum near to the ileo-cæcal valve. They are met with in two conditions, viz., either scattered singly, in which case they are termed *glandulæ solitariæ*, or aggregated in groups varying from one to three inches in length and about half-an-inch in width, chiefly of an oval form, their long axis parallel with that of the intestine. In this state, they are named *glandulæ agminatæ*, the groups being commonly called *Peyer's patches* (fig. 189), and almost always placed opposite the attachment of the mesentery. In structure, and in function, there is no essential difference between the solitary glands and the individual bodies of which each group or patch is made up. They are really single or aggregated masses of adenoid tissue forming lymph-follicles. In the condition in which they have been most commonly examined, each gland appears as a circular opaque-white rounded body, from $\frac{1}{24}$ to $\frac{1}{12}$ inch in diameter, according to the degree in which it is developed. They are principally contained in the submucous coat, but sometimes project through the *muscularis mucosæ* into the mucous membrane. In the agminate glands, each follicle reaches the free surface of the intestine, and is covered with columnar epithelium. Each gland is surrounded by the openings of Lieberkühn's follicles.

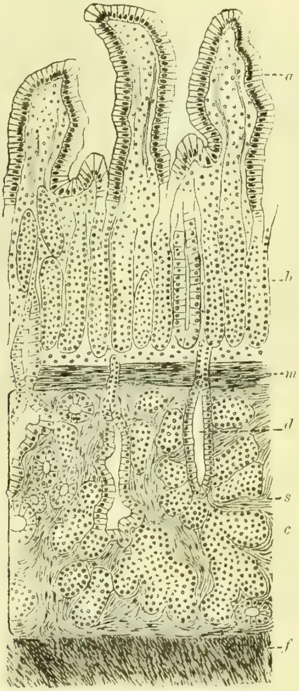

Fig. 188.—*Vertical section of duodenum*, showing *a*, villi; *b*, crypts of Lieberkühn, and *c*, Brunner's glands in the submucosa *s*, with ducts, *d*; muscularis mucosæ, *m*; and circular muscular coat *f*. (Schofield.)

The adjacent glands of a Peyer's patch are connected together by adenoid tissue. Sometimes the lymphoid tissue reaches the free surface, replacing the epithelium, as is also the case with some of the lymphoid follicles of the tonsil (p. 291).

Peyer's glands are surrounded by lymphatic sinuses which do not penetrate into their interior; the interior is, however, traversed by a very rich blood capillary plexus. If the vermiform appendix of a rabbit, which consists largely of Peyer's glands, be injected with blue, by pressing the point of a fine syringe into one of the lymphatic sinuses, the Peyer's glands will appear as greyish white spaces surrounded by blue; if now the arteries of the same be injected with red, the greyish patches will change to red, thus proving that they are *surrounded* by lymphatic spaces, but *penetrated* by blood-vessels. The lacteals passing out of the villi communicate with the lymph sinuses round Peyer's glands.

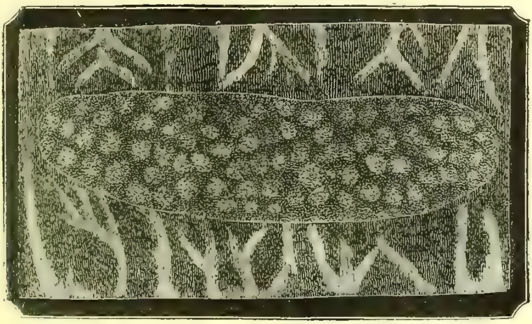

Fig. 189.—*Agminate follicles*, or *Peyer's patch*, in a state of distension. × 5. (Boehm.)

It is to be noted that they are largest and most prominent in children and young persons.

Villi.—The *Villi* (figs. 183, 188, 190, and 191), are confined exclusively to the mucous membrane of the *small* intestine. They are minute vascular processes, from a quarter of a line to a line and two-thirds in length, covering the surface of the mucous membrane, and giving it a peculiar velvety, fleecy appearance. Krause estimates them at fifty to ninety in number in a square line, at the upper part of the small intestine, and at forty to seventy in the same area at the lower part. They vary in form even in the same animal, and differ according as the lymphatic vessels they contain are empty or full of chyle; being usually, in the former case, flat and pointed at their summits, in the latter cylindrical or cleavate.

Each villus consists of a small projection of mucous membrane, and its interior is therefore supported throughout by fine adenoid tissue, which forms the framework or stroma in which the other constituents are contained.

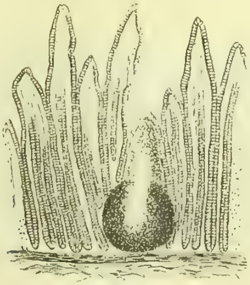

Fig. 190.—*Section of small intestine* showing villi, Lieberkühn's glands and a Peyer's solitary gland. *m*, *m*, muscularis mucosæ. (Klein and Noble Smith.)

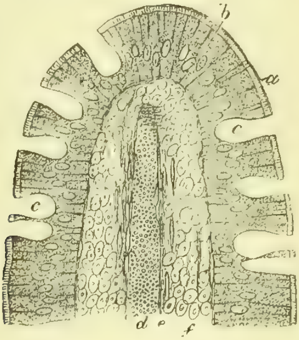

Fig. 191.—*Vertical section of a villus of the small intestine of a cat.* *a*, striated basilar border of the epithelium; *b*, columnar epithelium; *c*, goblet cells; *d*, central lymph-vessel; *e*, smooth muscular fibres; *f*, adenoid stroma of the villus in which lymph corpuscles lie. (Klein.)

The surface of the villus is clothed by columnar epithelium, which rests on a fine basement membrane; while within this are found, reckoning from without inwards, blood-vessels, fibres of the *muscularis mucosæ*, and a single lymphatic or lacteal vessel rarely looped or branched (fig. 192); besides granular matter, fat-globules, etc.

The *epithelium* is of the columnar kind, and continuous with that lining the other parts of the mucous membrane. The cells are arranged with their long axis radiating from the surface of the villus (fig. 191), and their smaller ends resting on the basement membrane. The free surface of the epithelial cells of the villi, like that of the cells which cover the general surface of the mucous membrane, is covered by a fine border which exhibits very delicate striations, whence it derives its name, "striated basilar border."

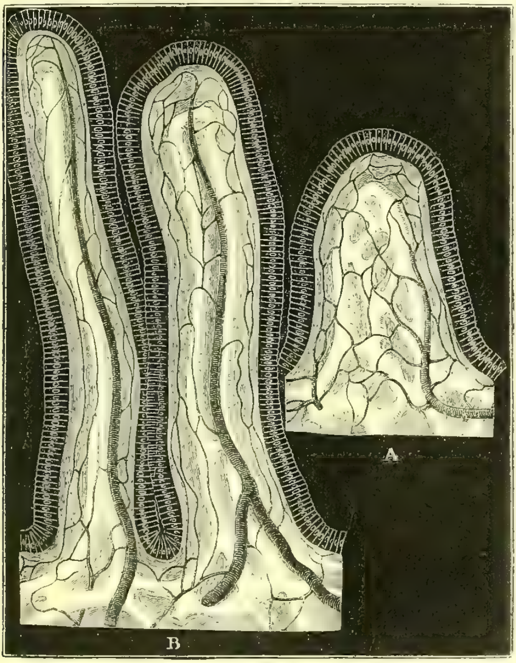

Fig. 192.—A. *Villus of sheep.* B. *Villi of man.* (Slightly altered from Teichmann.)

Beneath the basement or limiting membrane there is a rich supply of *blood-vessels.* Two or more minute arteries are distributed within each villus; and from their capillaries, which form a dense network, proceed one or two small veins, which pass out at the base of the villus.

The layer of the *muscularis mucosæ* in the villus forms a kind of thin hollow cone immediately around the central lacteal, and is, therefore, situate beneath the blood-vessels. It is without doubt instrumental in the propulsion of chyle along the lacteal.

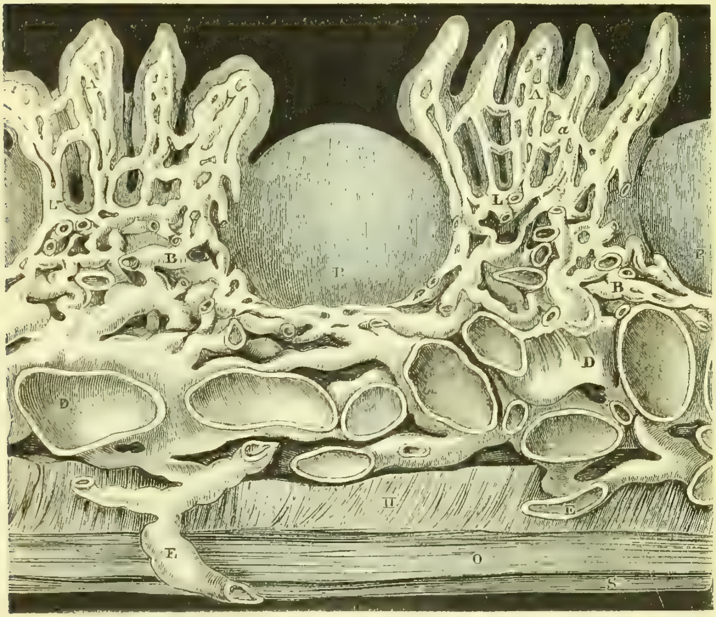

Fig. 193.—*Diagram of lacteal vessels in small intestine.* A, lacteals in villi; P, Peyer's glands; B and D, superficial and deep network of lacteals in submucous tissue; L, Lieberkühn's glands; E, small branch of lacteal vessel on its way to mesenteric gland; H and O, muscular fibres of intestine; S, peritoneum. (Teichmann.)

The *lacteal vessel* enters the base of each villus, and passing up in the middle of it, extends nearly to the tip, where it ends commonly by a closed and somewhat dilated extremity. In the larger villi there may be two small lacteal vessels which end by a loop (fig. 192), or the lacteals may form a kind of network in the villus. The last method of ending, however, is rarely or never seen in the human subject, although common in some of the lower animals (A, fig. 192).

The office of the villi is the absorption of chyle and other liquids from the intestine. The mode in which they effect this will be considered in the Chapter on ABSORPTION.

II. The Large Intestine.—The Large Intestine, which in an adult is from about 4 to 6 feet long, is subdivided for descriptive purposes into three portions (fig. 165) viz. :—the *cæcum*, a short wide pouch, communicating with the lower end of the small intestine through an opening, guarded by the *ileo-cæcal* valve; the *colon*, continuous with the cæcum, which forms the principal part of the large intestine, and is divided into an ascending, transverse, and descending portion; and the *rectum*, which, after dilating at its lower part, again contracts, and immediately afterwards opens externally through the *anus*. Attached to the cæcum is the small *appendix vermiformis*.

Structure.—Like the *small* intestine, the *large* is constructed of four principal coats, viz., the serous, muscular, submucous, and mucous. The *serous* coat need not be here particularly described. Connected with it are the small processes of peritoneum, containing fat, called *appendices epiploicæ*. The fibres of the *muscular* coat, like those of the small intestine, are arranged in two layers —the outer longitudinal, the inner circular. In the cæcum and colon, the longitudinal fibres, besides being, as in the small intestine, thinly disposed in all parts of the wall of the bowel, are collected, for the most part, into three strong bands, which being shorter, from end to end, than the other coats of the intestine, hold the canal in folds, bounding intermediate sacculi. On the division of these bands, the intestine can be drawn out to its full length, and it then assumes, of course, an uniformly cylindrical form. In the rectum, the fasciculi of these longitudinal bands spread out and mingle with the other longitudinal fibres, forming with them a thicker layer of fibres than exists on any other part of the intestinal canal. The circular muscular fibres are spread over the whole surface of the bowel, but are somewhat more marked in the intervals between the sacculi. Towards the lower end of the rectum they become more numerous, and at the anus they form a strong band called the *internal sphincter* muscle.

The *mucous membrane* of the large, like that of the small intestine, is lined throughout by columnar epithelium, but, unlike it, is quite smooth and destitute of villi, and is not projected in the form of *valvulæ conniventes.* Its general microscopic structure resembles that of the small intestine : and it is bounded below by the *muscularis mucosæ.*

The general arrangement of ganglia and nerve-fibres in the large intestine resembles that in the small (p. 315).

Glands of the Large Intestine.—The glands with which the large intestine is provided are of two kinds, (1) the *tubular* and (2) the *lymphoid.*

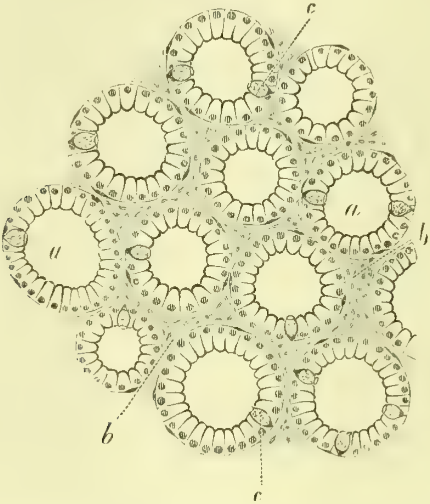

Fig. 194.—*Horizontal section through a portion of the mucous membrane of the large intestine,* showing Lieberkühn's glands in transverse section. *a*, lumen of gland—lining of columnar cells with *c*, goblet cells, *b*, supporting connective tissue.' Highly magnified. (V. D. Harris.)

(1.) The *tubular* glands, or glands of Lieberkühn, resemble those of the small intestine, but are somewhat larger and more numerous. They are also more uniformly distributed.

(2.) Follicles of *adenoid* or *lymphoid* tissue are most numerous in the cæcum and vermiform appendix. They resemble in shape and structure, almost exactly, the solitary glands of the small intestine. Peyer's patches are not found in the large intestine.

Ileo-cæcal Valve.—The ileo-cæcal valve is situate at the place of junction of the small with the large intestine, and guards against any reflex of the contents of the latter into the ileum. It is composed of two semilunar folds of mucous membrane

Each fold is formed by a doubling inwards of the mucous membrane, and is strengthened on the outside by some of the circular muscular fibres of the intestine, which are contained between the outer surfaces of the two layers of which each fold is composed. While the circular muscular fibres, however, of the bowel at the junction of the ileum with the cæcum are contained between the outer opposed surfaces of the folds of mucous membrane which form the valve, the longitudinal muscular fibres and the peritoneum of the small and large intestine respectively are continuous with each other, without dipping in to follow the circular fibres and the mucous membrane. In this manner, therefore, the folding inwards of these two last-named structures is preserved, while, on the other hand, by dividing the longitudinal muscular fibres and the peritoneum, the valve can be made to disappear, just as the constrictions between the sacculi of the large intestine can be made to disappear by performing a similar operation. The inner surface of the folds is smooth ; the mucous membrane of the ileum being continuous with that of the cæcum. That surface of each fold which looks towards the small intestine is covered with villi, while that which looks to the cæcum has none. When the cæcum is distended, the margin of the folds are stretched, and thus are brought into firm apposition one with the other.

Digestion in the Intestines.

After the food has been duly acted upon by the stomach, such as has not been absorbed passes into the duodenum, and is there subjected to the action of the secretions of the pancreas and liver, which enter that portion of the small intestine. Before considering the changes which the food undergoes in consequence, attention should be directed to the structure and secretion of these glands, and to the secretion (succus entericus) which is poured out into the intestines from the glands lining them.

The Pancreas, and its Secretion.

The Pancreas is situated within the curve formed by the duodenum; and its main duct opens into that part of the small intestine, through a small opening, or through a duct common to it and to the liver, about two and a half inches from the pylorus.

Structure.—In structure the pancreas bears some resemblance to the salivary glands. Its capsule and septa, as well as the blood-vessels and lymphatics, are similarly distributed. It is, however, looser and softer, the lobes and lobules being less compactly arranged. The main duct divides into branches (lobar ducts), one for each lobe, and these branches subdivide into intralobular ducts, and these again by their division and branching form the gland tissue proper. The intralobular ducts correspond to a lobule, while between them and the secreting tubes or *alveoli* are longer or shorter *intermediary* ducts. The larger ducts possess a very distinct lumen and a membrana propria lined with columnar epithelium, the cells of which are longitudinally striated, but are shorter than those found in the ducts of the salivary glands. In the intralobular ducts the epithelium is short and the lumen is smaller. The intermediary ducts opening into the alveoli possess a distinct lumen, with a membrana propria lined with a single layer of flattened elongated cells. The alveoli are branched and convoluted tubes, with a membrana propria lined with a single layer of columnar cells. They have no distinct lumen, its place being taken by fusiform or branched cells. Heidenhain has observed that the alveolar cells in the pancreas of a fasting dog

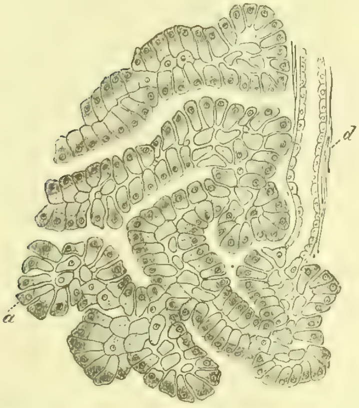

Fig. 195.—*Section of the pancreas of a dog during digestion.* *a*, alveoli lined with cells, the outer zone of which is well stained with hæmatoxylin; *d*, intermediary duct lined with squamous epithelium. × 350. (Klein and Noble Smith.)

consist of two zones, an inner or central zone, which is finely granular, and which stains feebly, and a smaller parietal zone of finely striated protoplasm, which stains easily. The nucleus is partly in one, partly in the other zone. During digestion, it is found that the outer zone increases in size, and the central zone diminishes; the cell itself becoming smaller from the discharge of the secretion. At the end of digestion the first condition again appears, the inner zone enlarging at the expense of the outer. It appears that the granules are formed by the protoplasm of the cells, from material supplied to it by the blood. The granules are thought to be not the ferment itself, but material from which, under certain conditions, the ferments of the gland are made, and therefore called *Zymogen.*

Pancreatic Secretion.—The secretion of the pancreas has been obtained for purposes of experiment from the lower animals, especially the dog, by opening the abdomen and exposing the duct of the gland, which is then made to communicate with the exterior. A pancreatic fistula is thus established.

An extract of pancreas made from the gland, which has been removed from an animal killed during digestion, possesses the active properties of pancreatic secretion. It is made by first dehydrating the gland, which has been cut up into small pieces, by keeping it for some days in absolute alcohol, and then, after the entire removal of the alcohol, placing it in strong glycerin. A glycerin extract is thus obtained. It is a remarkable fact, however, that the amount of the ferment *trypsin* greatly increases if the gland be exposed to the air for twenty-four hours before placing in alcohol; indeed, a glycerin extract made from the gland immediately upon removal from the body often appears to contain none of that ferment. This seems to indicate that the conversion of zymogen in the gland into the ferment only takes place during the act of secretion, and that the gland, although it always contains in its cells the materials (trypsinogen) out of which trypsin is formed, yet the conversion of the one into the other only takes place by degrees. Dilute acid appears to assist and accelerate the conversion, and if a recent pancreas be rubbed up with dilute acid before dehydration, a glycerin extract made afterwards, even though the gland may have been only recently removed from the body, is very active.

Properties.—Pancreatic juice is colourless, transparent, and slightly viscid, alkaline in reaction. It varies in specific gravity from 1010 to 1015, according to whether it is obtained from a permanent fistula—then more watery—or from a newly-opened duct. The solids vary in a temporary fistula from 80 to 100 parts per thousand, and in a permanent one from 16 to 50 per thousand.

Chemical Composition of the Pancreatic Secretion.

From a permanent fistula. (Bernstein.)

Water		975
Solids—Ferments:		
Proteids, including Serum—Albumin, Casein, Leucin and Tyrosin, Fats and Soaps	17	
Inorganic residue, especially Sodium Carbonate	8	25
		1000

Functions.—(1.) It converts *proteids into peptones*, the intermediate product being not akin to syntonin or acid-albumin, as in gastric digestion, but to alkali-albumin. Kühne believes that the intermediate products, both in the peptic and pancreatic digestion of proteids, are two, viz., antialbumose and hemialbumose, and that the peptones formed correspond to these, viz., antipeptone and hemipeptone. The hemipeptone is capable of being converted by the action of the pancreatic ferment—*trypsin*—into leucin and tyrosin, but is not so changed by pepsin; the antipeptone cannot be further split up. The products of pancreatic digestion are sometimes further complicated by the appearance of certain fæcal substances, of which indol and naphthilamine are the most important. (Kühne.)

When the digestion goes on for a long time the indol is formed in considerable quantities, and emits a most disagreeable fæcal odour, which was attributed to putrefaction till Kühne showed its true nature. All the albuminous or proteid substances which have not been converted into peptone, and absorbed in the stomach, and the partially changed substances, *i.e.*, the parapeptones, are converted into peptone by the pancreatic juice, and then in part into leucin and tyrosin.

(2.) *Nitrogenous bodies other than proteids, are not to any extent altered.* Mucin can, however, be dissolved, but not gelatin or horny tissues.

(3.) *Starch is converted into glucose* in an exactly similar manner to that which happens with the saliva. As mentioned before, it seems not unlikely that glucose is not formed at once from starch, but that certain dextrines are intermediate products. If the sugar which is at first formed, as is stated by some chemists, be not glucose but maltose, at any rate the pancreatic juice after a time completes the whole change of starch into glucose. There is a distinct amylolytic ferment (Amylopsin) in the pancreatic juice which cannot be distinguished from ptyalin.

(4.) *Oils and fats are both emulsified and split up into their fatty acids and glycerin by pancreatic secretion.* Even if part of this action is due to the alkinity of the medium, it is probable that there is a third distinct ferment (Steapsin) which facilitates the change.

Several cases have been recorded in which the pancreatic duct being obstructed, so that its secretion could not be discharged, fatty or oily matter was abundantly discharged from the intestines. In nearly all these cases, indeed, the liver was coincidently diseased, and the change or absence of the bile might appear to contribute to the result; yet the frequency of extensive disease of the liver, unaccompanied by fatty discharges from the intestines, favours the view that, in these cases, it is to the absence of the pancreatic fluid from the intestines that the excretion or non-absorption of fatty matter should be ascribed.

(5.) *It possesses the property of curdling milk,* containing a special (rennet) ferment for that purpose. The ferment is distinct from trypsin, and will act in the presence of an acid (W. Roberts).

Conditions favourable to the Action of the Pancreatic Juice.—These are similar to those which are favourable to the action of the saliva, and the reverse (p. 285).

The Liver.

The Liver, the largest gland in the body, situated in the abdomen, chiefly on the right side, is an extremely vascular organ, and receives its supply of blood from two distinct vessels, the *portal vein* and *hepatic artery*, while the blood is returned from it into the vena cava inferior by the *hepatic veins.* Its secretion, the *bile*, is conveyed from it by the *hepatic duct*, either directly into the intestine, or, when digestion is not going on, into the *cystic* duct, and thence into the gall-bladder, where it accumulates until required. The portal vein, hepatic artery, and hepatic duct branch together throughout the liver, while the hepatic veins and their tributaries run by themselves.

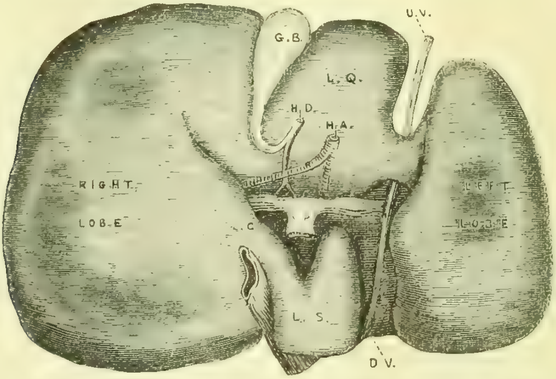

Fig. 196.—*The under surface of the liver.* G. B., gall-bladder; H. D., common bile-duct; H. A., hepatic artery; V. P., portal vein; L. Q., lobulus quadratus; L. S., lobulus spigelii; L. C., lobulus caudatus; D. V., ductus venosus; U. V., umbilical vein. (Noble Smith.)

On the outside the liver has an incomplete covering of peritoneum, and beneath this is a very fine coat of areolar tissue, continuous over the whole surface of the organ. It is thickest where the peritoneum is absent, and is continuous on the general surface of the liver with the fine, and, in the human subject, almost imperceptible, areolar tissue investing the lobules. At the transverse fissure it is merged in the areolar investment called Glisson's capsule, which, surrounding the portal vein, hepatic artery, and hepatic duct, as they enter at this part, accompanies them in their branchings through the substance of the liver.

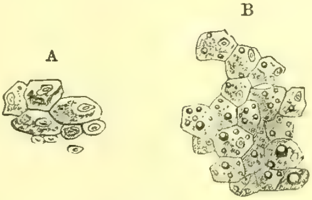

Fig. 197.—A. *Liver-cells.* B. Ditto, containing various sized particles of fat.

Structure.—The liver is made up of small roundish or oval portions called *lobules*, each of which is about $\frac{1}{20}$ of an inch in diameter, and composed of the minute branches of the portal vein, hepatic artery, hepatic duct, and hepatic vein; while the interstices of these vessels are filled by the liver cells. The hepatic cells (fig. 197), which form the glandular or secreting part of the liver, are of a spheroidal form, somewhat polygonal from mutual pressure about $\frac{1}{800}$ to $\frac{1}{1000}$ inch in diameter, possessing one, sometimes two nuclei. The cell-substance contains numerous fatty molecules, and some yellowish-brown granules of bile-pigment.

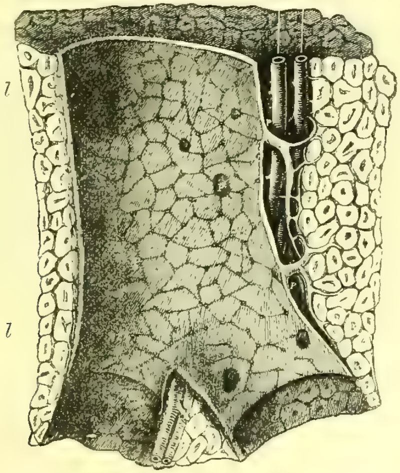

Fig. 198.—*Longitudinal section of a portal canal*, containing a portal vein, hepatic artery and hepatic duct, from the pig. P, branch of vena portæ, situate in a portal canal formed amongst the lobules of the liver, *l l*, and giving off vaginal branches; there are also seen within the large portal vein numerous orifices of the smallest interlobular veins arising directly from it; *a*, hepatic artery; *d*, hepatic duct. × 5. (Kiernan.)

The cells sometimes exhibit slow amœboid movements. They are held together by a very delicate sustentacular tissue, continuous with the interlobular connective tissue.

To understand the distribution of the blood-vessels in the liver, it will be well to trace, first, the two blood-vessels and the duct which enter the organ on the under surface at the transverse fissure, viz., the portal vein, hepatic artery, and hepatic duct. As before remarked, all three run in company, and their appearance on longitudinal section is shown in fig. 198. Running together through the substance of the liver, they are contained in small channels called *portal canals*, their immediate investment being a sheath of areolar tissue (Glisson's capsule).

To take the distribution of the portal vein first:—In its course through the liver this vessel gives off small branches which divide and subdivide between the lobules surrounding them and limiting them, and from this circumstance called *inter*-lobular veins. From these small vessels a dense capillary network is prolonged into the substance of the lobule, and this network, gradually gathering itself up, so to speak, into larger

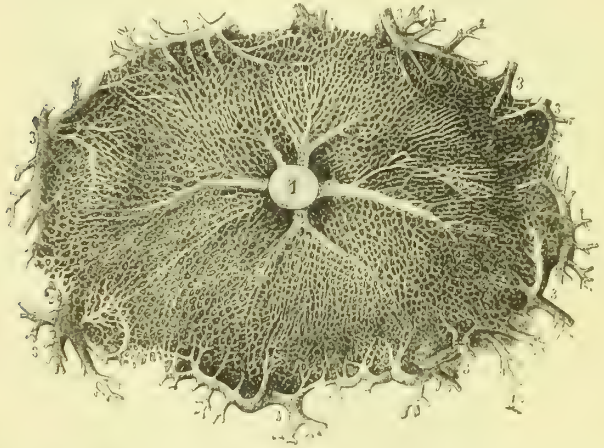

Fig. 199.—*Cross section of a lobule of the human liver*, in which the capillary network between the portal and hepatic veins has been fully injected. 1, section of the *intra*-lobular vein; 2, its smaller branches collecting blood from the capillary network; 3, *inter*-lobular branches of the vena portæ with their smaller ramifications passing inwards towards the capillary network in the substance of the lobule. × 60. (Sappey.)

vessels, converges finally to a single small vein, occupying the centre of the lobule, and hence called *intra*-lobular. This arrangement is well seen in fig. 199, which represents a transverse section of a lobule.

The small *intra*-lobular veins discharge their contents into veins called *sub*-lobular (*h h h*, fig. 200); while these again, by their union, form the main branches of the *hepatic* veins, which leave the posterior border of the liver to end by two or three principal trunks in the inferior vena cava, just before its passage through the diaphragm. The *sub*-lobular and *hepatic veins*, unlike the *portal* vein and its companions, have little or no areolar tissue around them, and their coats being very thin, they form little more than mere channels in the liver substance which closely surrounds them.

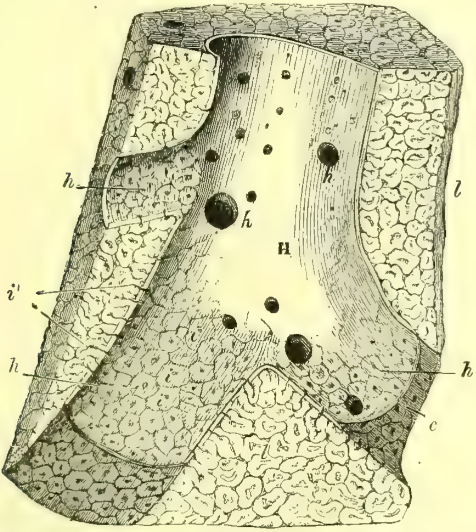

Fig. 200.—*Section of a portion of liver passing longitudinally through a considerable hepatic vein*, from the pig. H, hepatic venous trunk, against which the sides of the lobules (*l*) are applied; *h*, *h*, *h*, sublobular hepatic veins, on which the bases of the lobules rest, and through the coats of which they are seen as polygonal figures; *i*, mouth of the intralobular veins, opening into the sublobular veins; *i'*, intralobular veins shown passing up the centre of some divided lobules; *l*, *l*, cut surface of the liver; *c*, *c*, walls of the hepatic venous canal, formed by the polygonal bases of the lobules. × 5. (Kiernan.)

The manner in which the lobules are connected with the *sub-lobular* veins by means of the small *intra-lobular* veins is well-seen in the diagram (fig. 200 and in fig. 201), which represent the parts as seen in a longitudinal section. The appearance has been likened to a twig having leaves without footstalks—the lobules representing the leaves, and the *sub-lobular* vein the small branch from which it springs. On a transverse section, the appearance of the *intra-lobular* veins is that of 1, fig. 199, while both a transverse and longitudinal section are exhibited in fig. 176.

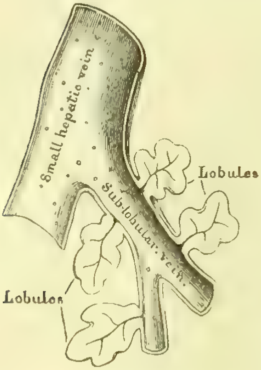

Fig. 201.—*Diagram showing the manner in which the lobules of the liver rest on the sublobular veins.* (After Kiernan.)

The hepatic artery, the function of which is to distribute blood for nutrition to Glisson's capsule, the walls of the ducts and blood-vessels, and other parts of the liver, is distributed in a very similar manner to the portal vein, its blood being returned by small branches either into the ramifications of the portal vein, or into the capillary plexus of the lobules which connects the *inter-* and *intra-*lobular veins.

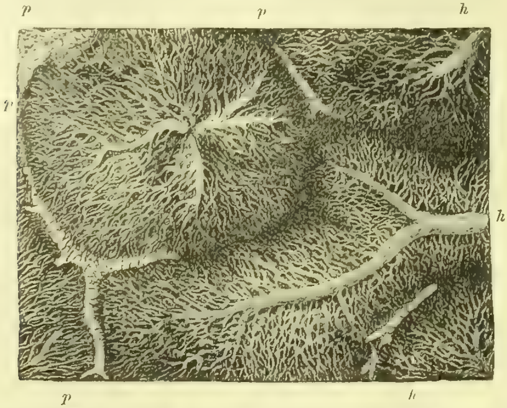

Fig. 202.—*Capillary network of the lobules of the rabbit's liver.* The figure is taken from a very successful injection of the hepatic veins, made by Harting: it shows nearly the whole of two lobules, and parts of three others; *p*, portal branches running in the interlobular spaces; *h*, hepatic veins penetrating and radiating from the centre of the lobules. × 45. (Kölliker.)

The hepatic duct divides and subdivides in a manner very like that of the portal vein and hepatic artery, the larger branches being lined by *cylindrical*, and the smaller by small *polygonal* epithelium.

The bile-capillaries commence between the hepatic cells, and are bounded by a delicate membranous wall of their own. They appear to be always bounded by hepatic cells on all sides, and are thus separated from the nearest blood-capillary by at least the breadth of one cell (figs. 203 and 204).

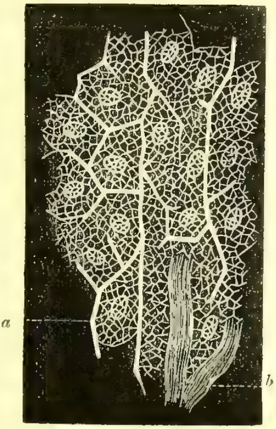

Fig. 203.—*Portion of a lobule of liver.* *a*, bile capillaries between liver-cells, the network in which is well seen; *b*, blood capillaries. × 350. (Klein and Noble Smith.)

The Gall-bladder.—The Gall-bladder (G, B, fig. 196) is a pyriform bag, attached to the under surface of the liver, and supported also by the peritoneum, which passes below it. The larger end or *fundus*, projects beyond the front margin of the liver; while the smaller end contracts into the cystic duct.

Structure.—The walls of the gall-bladder are constructed of three principal coats. (1) Externally (excepting that part which is in contact with the liver), is the *serous* coat, which has the same structure as the peritoneum with which it is continuous. Within this is (2) the *fibrous* or areolar coat, constructed of tough fibrous

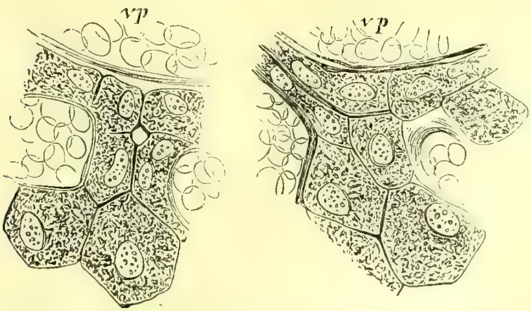

Fig. 204.—*Hepatic cells and bile capillaries*, from the liver of a child three months old. Both figures represent fragments of a section carried through the periphery of a lobule. The red corpuscles of the blood are recognized by their circular contour: *vp*, corresponds to an interlobular vein in immediate proximity with which are the epithelial cells of the biliary ducts, to which, at the lower part of the figures, the much larger hepatic cells suddenly succeed. (E. Hering.)

and elastic tissue, with which is mingled a considerable number of plain muscular fibres, both longitudinal and circular. (3) Internally the gall-bladder is lined by mucous membrane, and a layer of columnar epithelium. The surface of the mucous membrane presents to the naked eye a minutely honeycombed appearance from a number of tiny polygonal depressions with intervening ridges, by which its surface is mapped out. In the cystic duct the mucous membrane is raised up in the form of crescentic folds, which together appear like a spiral valve, and which minister to the function of the gall-bladder in retaining the bile during the intervals of digestion.

The gall-bladder and all the main biliary ducts are provided with mucous glands, which open on their internal surface.

Functions of the Liver.—The functions of the Liver may be classified under the following heads:—1. The Secretion of Bile. 2. The Elaboration of Blood; under this head may be included the Glycogenic Function.

I. The Secretion of Bile.

Properties of the Bile.—The bile is a somewhat viscid fluid, of a yellow or reddish-yellow colour, a strongly bitter taste, and, when fresh, with a scarcely perceptible odour: it has a neutral or slightly alkaline reaction, and its specific gravity is about 1020. Its colour and degree of consistence vary much, apparently independent of disease; but, as a rule, it becomes gradually more deeply coloured and thicker as it advances along its ducts, or when it remains long in the gall-bladder, wherein, at the same time, it becomes more viscid and ropy, of a darker colour, and more bitter taste, mainly from its greater degree of concentration, on account of partial absorption of its water, but partly also from being mixed with mucus.

Chemical Composition of Human Bile. (Frerichs.)

Water	859·2
Solids	140·8
	1000·0

Bile salts or Bilin	91·5
Fat	9·2
Cholesterin	2·6
Mucus and colouring matters	29·8
Salts	7·7
	140·8

Bile salts, or *Bilin*, can be obtained as colourless, exceedingly deliquescent crystals, soluble in water, alcohol, and alkaline solutions, giving to the watery solution the taste and general characters of bile. They consist of sodium salts of glycocholic and taurocholic acids. The former salt is composed of cholic acid conjugated with glycin (see Appendix), the latter of the same acid conjugated with taurin. The proportion of these two salts in the bile of different animals varies, *e.g.*, in ox bile the glycocholate is in great excess, whereas the bile of the dog, cat, bear, and other carnivora contains taurocholate alone; in human bile both are present in about the same amount (glycocholate in excess ?).

Preparation of Bile Salt.—Bile salts may be prepared in the following manner: mix bile which has been evaporated to a quarter of its bulk with animal charcoal, and evaporate to perfect dryness in a water bath. Next extract the mass whilst still warm with absolute alcohol. Separate the alcoholic extract by filtration, and to it add perfectly anhydrous ether as long as a precipitate is thrown down. The solution and precipitate should be set aside in a closely stoppered bottle for some days, when crystals of the bile salts or bilin will have separated out. The glycocholate may be separated from the taurocholate by dissolving bilin in water, and adding to it a solution of neutral lead acetate, and then a little basic lead acetate, when lead glycocholate separates out. Filter and add to the filtrate lead acetate and ammonia, a precipitate of lead taurocholate will be formed, which may be filtered off. In both cases, the lead may be got rid of by suspending or dissolving in hot alcohol, adding hydrogen sulphate, filtering and allowing the acids to separate out by the addition of water.

The test for bile salts is known as Pettenkofer's. If to an aqueous solution of the salts strong sulphuric acid be added, the bile acids are first of all precipitated, but on the further addition of the acid are re-dissolved. If to the solution a drop of solution of cane sugar be added, a fine purple colour is developed.

The re-action will also occur on the addition of grape or fruit sugar instead of cane sugar, slowly with the first, quickly with the last; and a colour similar to the above is produced by the action of sulphuric acid and sugar on albumen, the crystalline lens, nerve tissue, oleic acid, pure ether, cholesterin, morphia, codeia and amylic alcohol.

The spectrum of Pettenkofer's reaction, when the fluid is moderately diluted, shows four bands—the most marked and largest at E, and a little to the left; another at F.; a third between D and E, nearer to D; and the fourth near D.

The yellow *colouring matter* of the bile of man and the Carnivora is termed *Bilirubin* or *Bilifulvin* ($C_{16}\ H_{18}\ N_2\ O_3$) crystallizable and insoluble in water, soluble in chloroform or carbon disulphate; a green colouring matter, *Biliverdin* ($C_{16}\ H_{20}\ N_2\ O_5$), which always exists in large amount in the bile of Herbivora, being formed from bilirubin on exposure to the air, or by subjecting the bile to any other oxidizing agency, as by adding nitric acid. When the bile has been long in the gall-bladder, a third pigment, *Biliprasin*, may be also found in small amount.

In cases of biliary obstruction, the colouring matter of the bile is re-absorbed, and circulates with the blood, giving to the tissues the yellow tint characteristic of jaundice.

The colouring matters of human bile do not appear to give characteristic absorption spectra; but the bile of the guinea pig, rabbit, mouse, sheep, ox, and crow do so, the most constant of which appears to be a band at F. The bile of the sheep and ox give three bands in a thick layer, and four or five bands with a thinner layer, one on each side of D, one near E, and a faint line at F. (McMunn).

There seems to be a close relationship between the colour-matter of the blood and of the bile, and it may be added, between these and that of the urine (urobilin), and of the fæces (stercobilin) also; it is probable they are, all of them, varieties of the same pigment, or derived from the same source. Indeed it is maintained that *Urobilin* is identical with *Hydrobilirubin*, a substance which is obtained from bilirubin by the action of sodium amalgam, or by the action of sodium amalgam on alkaline hæmatin; both urobilin and hydrobilirubin giving a characteristic absorption band between b and F. They are also identical with stercobilin, which is formed in the alimentary canal from bile pigments.

A common *test* (Gmelin's) for the presence of *bile-pigment* consists of the addition of a small quantity of nitric acid, yellow with nitrous acid; if bile be present, a play of colours is produced, beginning with green and passing through blue and violet to red, and lastly to yellow. The spectrum of Gmelin's test gives a black band extending from near b to beyond F.

Fatty substances are found in variable proportions in the bile. Besides the ordinary saponifiable fats, there is a small quantity of *Cholesterin*, a so-called non-saponifiable fat, which, with the other free fats, is probably held in solution by the bile salts. It is a body belonging to the class of monatomic alcohols ($C_{26} H_{44} O$), and crystallizes in rhombic plates (fig. 205). It is insoluble in water and cold alcohol, but dissolves easily in boiling alcohol or ether. It gives a red colour with strong sulphuric acid, and with nitric acid and ammonia; also a play of colours beginning with blood red and ending with green on the addition of sulphuric acid and chloroform. *Lecithin* ($C_{44} H_{90} NPO_9$), a phosphorus-containing body and *Neurin* ($C_5 H_{15} NO_2$), are also found in bile, the latter probably as a decomposition product of the former.

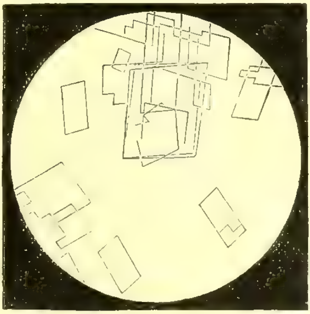

Fig. 205.—*Crystalline scales of cholesterin.*

The *Mucus* in bile is derived from the mucous membrane and glands of the gall-bladder, and of the hepatic ducts. It constitutes the residue after bile is treated with alcohol. The epithelium with which it is mixed may be detected in the bile with the microscope in the form of cylindrical cells, either scattered or still held together in layers. To the presence of the mucus is probably to be ascribed the rapid decomposition undergone by the bilin; for, according to Berzelius, if the mucus be separated, bile will remain unchanged for many days.

The *Saline* or *inorganic constituents* of the bile are similar to those found in most other secreted fluids. It is possible that the carbonate and neutral phosphate of sodium and potassium, found in the ashes of bile, are formed in the incineration, and do not exist as such in the fluid. Oxide of iron is said to be a common constituent of the ashes of bile, and copper is generally found in healthy bile, and constantly in biliary calculi.

Gas—A certain small amount of carbonic acid, oxygen, and nitrogen, may be extracted from bile.

Mode of Secretion and Discharge.—The process of secreting bile is continually going on, but appears to be retarded during fasting, and accelerated on taking food. This has been shown by tying the common bile-duct of a dog, and establishing a fistulous opening between the skin and gall-bladder, whereby all the bile secreted was discharged at the surface. It was noticed that when the animal was fasting, sometimes not a drop of bile was discharged for several hours; but that, in about ten minutes after the introduction of food into the stomach, the bile began to flow abundantly, and continued to do so during the whole period of digestion. (Blondlot, Bidder and Schmidt.)

The bile is formed in the hepatic cells; then, being discharged into the minute hepatic ducts, it passes into the larger trunks, and from the main hepatic duct may be carried at once into the duodenum. But, probably, this happens only while digestion is going on; during fasting, it regurgitates from the common bile-duct through the cystic duct, into the gall-bladder, where it accumulates till, in the next period of digestion, it is discharged into the intestine. The gall-bladder thus fulfils what appears to be its chief or only office, that of a reservoir; for its presence enables bile to be constantly secreted, yet insures its employment in the service of digestion, although digestion is periodic, and the secretion of bile constant.

The mechanism by which the bile passes into the gall-bladder is simple. The orifice through which the common bile-duct communicates with the duodenum is narrower than the duct, and appears to be closed, except when there is sufficient pressure behind to force the bile through it. The pressure exercised upon the bile secreted during the intervals of digestion appears insufficient to overcome the force with which the orifice of the duct is closed; and the bile in the common duct, finding no exit in the intestine, traverses the cystic duct, and so passes into the gall-bladder, being probably aided in this retrograde course by the peristaltic action of the ducts. The bile is discharged from the gall-bladder and enters the duodenum on the introduction of food into the small intestine: being pressed on by the contraction of the coats of the gall-bladder, and of the common bile-duct also; for both these organs contain unstriped muscular fibre-cells. Their contraction is excited by the stimulus of the food in the duodenum acting so as to produce a reflex movement, the force of which is sufficient to open the orifice of the common bile-duct.

Bile, as such, is not pre-formed in the blood. As just observed, it is formed by the hepatic cells, although some of the material may be brought to them almost in the condition for immediate secretion. When it is, however, prevented by an obstruction of some kind, from escaping into the intestine (as by the passage of a *gall-stone* along the hepatic duct) it is absorbed in great excess into the blood, and, circulating with it, gives rise to the well-known phenomena of jaundice. This is explained by the fact that the pressure of secretion in the ducts is normally very low, and if it exceeds $\frac{3}{5}$ inch of mercury (16 mm.) the secretion ceases to be poured out, and if the opposing force be increased, the bile finds its way into the blood.

Quantity.—Various estimates have been made of the *quantity* of bile discharged into the intestines in twenty-four hours: the quantity doubtless varying, like that of the gastric fluid, in proportion to the amount of food taken. A fair average of several computations would give 20 to 40 oz. (600 — 900 cc.) as the quantity daily secreted by man.

Uses.—(1) As an *excrementitious* substance, the bile may serve especially as a medium for the separation of excess of carbon and hydrogen from the blood; and its adaptation to this purpose is well-illustrated by the peculiarities attending its secretion and disposal in the fœtus. During intra-uterine life, the lungs and the intestinal canal are almost inactive; there is no respiration of open air or digestion of food; these are unnecessary, on account of the supply of well elaborated nutriment received by the vessels of the fœtus at the placenta. The liver, during the same time, is proportionately larger than it is after birth, and the secretion of bile is active, although there is no food in the intestinal canal upon which it can exercise any digestive property. At birth, the intestinal canal is full of thick bile, mixed with intestinal secretion; the *meconium*, or fæces of the fœtus, containing all the essential principles of bile.

Composition of Meconium (Frerichs):

Biliary resin	15·6
Common fat and cholesterin	15·4
Epithelium, mucus, pigment, and salts	69·0
	100·0

In the fœtus, therefore, the main purpose of the secretion of bile must be the purification of blood by *direct* excretion, *i.e.*, by separation from the blood, and ejection from the body without further change. Probably all the bile secreted in fœtal life is incorporated in the meconium, and with it discharged, and thus the liver may be said to discharge a function in some sense vicarious of that of the lungs. For, in the fœtus, nearly all the blood coming from the placenta passes through the liver, previous to its distribution to the several organs of the body; and the abstraction of carbon, hydrogen, and other elements of bile will purify it, as in extra-uterine life it is purified by the separation of carbonic acid and water at the lungs.

The evident disposal of the fœtal bile by excretion, makes it highly probable that the bile in extra-uterine life is also, at least in part, destined to be discharged as excrementitious. The analysis of the fæces of both children and adults shows that (except when rapidly discharged in purgation) they contain very little of the bile secreted, probably not more than one-sixteenth part of its weight, and that this portion includes chiefly its colouring, and some of its fatty matters, and to only a very slight degree, its salts, almost all of which have been re-absorbed from the intestines into the blood.

The elementary composition of bile salts shows, however, such a preponderance of carbon and hydrogen, that probably, after absorption, it combines with oxygen, and is excreted in the form of carbonic acid and water. The change after birth, from the direct to the indirect mode of excretion of the bile may, with much probability, be connected with a purpose in relation to the development of heat. The temperature of the fœtus is maintained by that of the parent, and needs no source of heat within itself; but, in extra-uterine life, there is (as one may say) a waste of material for heat when any excretion is discharged unoxidized; the carbon and hydrogen of the bilin, therefore, instead of being ejected in the fæces, are re-absorbed, in order that they may be combined with oxygen, and that in the combination heat may be generated.

A substance, which has been discovered in the fæces, and named *stercorin* is closely allied to cholesterin; and it has been suggested that while one great function of the liver is to excrete cholesterin from the blood, as the kidney excretes urea, the stercorin of fæces is the modified form in which cholesterin finally leaves the body. Ten grains and a half of stercorin are excreted daily (A. Flint).

From the peculiar manner in which the liver is supplied with much of the blood that flows through it, it is probable that this organ is excretory, not only for such hydro-carbonaceous matters as may need expulsion from any portion of the blood, but that it serves for the direct purification of the stream which, arriving by the portal vein, has just gathered up various substances in its course through the digestive organs—substances which may need to be expelled, almost immediately after their absorption. For it is easily conceivable that many things may be taken up during digestion, which not only are unfit for purposes of nutrition, but which would be positively injurious if allowed to mingle with the general mass of the blood. The liver, therefore, may be supposed placed in the only road by which such matters can pass unchanged into the general current, jealously to guard against their further progress, and turn them back again into an excretory channel. The frequency with which metallic poisons are either excreted by the liver, or intercepted and retained, often for a considerable time, in its own substance, may be adduced as evidence for the probable truth of this supposition.

(2). *As a digestive fluid.*—Though one chief purpose of the secretion of bile may thus appear to be the purification of the blood by ultimate excretion, yet there are many reasons for believing that, while it is in the intestines it performs an important part in the process of digestion. In nearly all animals, for example, the bile is discharged, not through an excretory duct communicating with the external surface or with a simple reservoir, as most excretions are, but is made to pass into the intestinal canal, so as to be mingled with the chyme directly after it leaves the stomach; an arrangement, the constancy of which clearly indicates that the bile has some important relations to the food with which it is thus mixed. A similar indication is furnished also by the fact that the secretion of bile is most active, and the quantity discharged into the intestines much greater, during digestion than at any other time; although, without doubt, this activity of secretion during digestion may, however, be in part ascribed to the fact that a greater quantity of blood is sent through the portal vein to the liver at this time, and that this blood contains some of the materials of the food absorbed from the stomach and intestines, which may need to be excreted, either temporarily, (to be afterwards re-absorbed,) or permanently.

Respecting the functions discharged by the bile in digestion, there is little doubt that it (*a.*) assists in *emulsifying the fatty portions* of the food, and thus rendering them capable of being absorbed by the lacteals. For it has appeared in some experiments in which the common bile-duct was tied, that, although the process of digestion in the stomach was unaffected, chyle was no longer well formed; the contents of the lacteals consisting of clear, colourless fluid, instead of being opaque and white, as they ordinarily are, after feeding.

(*b.*) It is probable, also, that the *moistening of the mucous membrane* of the intestines by bile facilitates absorption of fatty matters through it.

(*c.*) The bile, like the gastric fluid, has a considerable *antiseptic* power, and may serve to prevent the decomposition of food during the time of its sojourn in the intestines. Experiments show that the contents of the intestines are much more fœtid after the common bile-duct has been tied than at other times; moreover, it is found that the mixture of bile with a fermenting fluid stops or spoils the process of fermentation.

(*d.*) The bile has also been considered to act as a *natural purgative*, by promoting an increased secretion of the intestinal glands, and by stimulating the intestines to the propulsion of their contents. This view receives support from the constipation which ordinarily exists in jaundice, from the diarrhœa which accompanies excessive secretion of bile, and from the purgative properties of ox-gall.

(*e.*) The bile appears to have the power of *precipitating the gastric parapeptones and peptones, together with the pepsin* which is mixed up with them, as soon as the contents of the stomach meet it in the duodenum. The purpose of this operation is probably both to delay any change in the parapeptones until the pancreatic juice can act upon them, and also to prevent the pepsin from exercising its solvent action on the ferments of the pancreatic juice.

Nothing is known with certainty respecting the changes which the re-absorbed portions of the bile undergo. That they are much changed appears from the impossibility of detecting them in the blood; and that part of this change is effected in the liver is probable from an experiment of Magendie, who found that when he injected bile into the portal vein, a dog was unharmed, but was killed when he injected the bile into one of the systemic vessels.

II. The Liver as a Blood-elaborating Gland.

The secretion of bile, as already observed, is only one of the purposes fulfilled by the liver. Another very important function appears to be that of so acting upon certain constituents of the blood passing through it, as to render some of them capable of assimilation with the blood generally, and to prepare others for being duly eliminated in the process of respiration. It appears that the peptones, conveyed from the alimentary canal by the blood of the portal vein, require to be submitted to the influence of the liver before they can be assimilated by the blood; for if such albuminous matter is injected into the jugular vein, it speedily appears in the urine; but if introduced into the portal vein, and thus allowed to traverse the liver, it is no longer ejected as a foreign substance, but is incorporated with the albuminous part of the blood. Albuminous matters are also subject to decomposition by the liver in another way to be immediately noticed (p. 349). The formation of urea by the liver will be again referred to (p. 457).

Glycogenic Function.—One of the chief uses of the liver in connection with elaboration of the blood is comprised in what is known as its *glycogenic function.* The important fact that the liver normally forms *glucose* or grape sugar, or a substance readily convertible into it, was discovered by Claude Bernard in the course of some experiments which he undertook for the purpose of finding out in what part of the circulatory system the saccharine matter disappeared, which was absorbed from the alimentary canal. With this purpose he fed a dog for seven days with food containing a large quantity of sugar and starch; and, as might be expected, found sugar in both the portal and hepatic veins. He then fed a dog with meat only, and, to his surprise, still found sugar in the hepatic veins. Repeated experiments gave invariably the same result; no sugar being found, under a meat diet, in the portal vein, if care were taken, by applying a ligature on it at the transverse fissure, to prevent reflux of blood from the hepatic venous system. Bernard found sugar also in the substance of the liver. It thus seemed certain that the liver formed sugar, even when, from the absence of saccharine and amyloid matters in the food, none could be brought directly to it from the stomach or intestines.

Excepting cases in which large quantities of starch and sugar were taken as food, no sugar was found in the blood after it had passed through the lungs; the sugar formed by the liver, having presumably disappeared by combustion, in the course of the pulmonary circulation.

Bernard found, subsequently to the before-mentioned experiments, that a liver, removed from the body, and from which all sugar had been completely washed away by injecting a stream of water through its blood-vessels, will be found, after the lapse of a few hours, to contain sugar in abundance. This *post-mortem* production of sugar was a fact which could only be explained in the supposition that the liver contained a substance, readily convertible into sugar in the course merely of post-mortem decomposition; and this theory was proved correct by the discovery of a substance in the liver allied to starch, and now generally termed *glycogen.* We may believe, therefore, that the liver does not form sugar directly from the materials brought to it by the blood, but that glycogen is first formed and stored in its substance; and that the sugar, when present, is the result of the transformation of the latter.

Quantity of Glycogen formed.—Although, as before mentioned, glycogen is produced by the liver when neither starch nor sugar is present in the food, its amount is much less under such a diet.

Average amount of Glycogen in the Liver of Dogs under various Diets (Pavy).

Diet.	Amount of Glycogen in Liver.
Animal food	7·19 per cent.
Animal food with sugar (about ¼ lb. of sugar daily)	14·5 ,,
Vegetable diet (potatoes, with bread or barley-meal)	17·23 ,,

The dependence of the formation of glycogen on the food taken is also well shown by the following results, obtained by the same experimenter:—

Average quantity of Glycogen found in the Liver of Rabbits after Fasting and after a diet of Starch and Sugar respectively.

	Average amount of Glycogen in Liver.
After fasting for three days	Practically absent.
,, diet of starch and grape-sugar . .	15·4 per cent.
,, ,, cane-sugar	16·9 ,,

Regarding these facts there is no dispute. All are agreed that glycogen is formed, and laid up in store, temporarily, by the liver-cells; and that it is not formed exclusively from saccharine and amylaceous foods, but from albuminous substances also; the albumen, in the latter case, being probably split up into glycogen, which is temporarily stored in the liver, and urea, which is excreted by the kidneys.

Destination of Glycogen.—There are two chief theories on the subject of the destination of glycogen. (1.) That the conversion of glycogen into sugar takes place rapidly during life by the agency of a ferment also formed in the liver: and the sugar is conveyed away by the blood of the hepatic veins, and soon undergoes combustion. (2.) That the conversion into sugar only occurs after death, and that during life no sugar exists in healthy livers; glycogen not undergoing this transformation. The chief arguments advanced in support of this view are, (*a*) that scarcely a trace of sugar is found in blood drawn during life from the right ventricle, or in blood collected from the right side of the heart *immediately* after an animal has been killed; while if the examination be delayed for a very short time after death, sugar in abundance may be found in such blood; (*b*), that the liver, like the venous blood in the heart, is, at the moment of death, completely free from sugar, although afterwards its tissue speedily becomes saccharine, unless the formation of sugar be prevented by freezing, boiling, or other means calculated to interfere with the action of a ferment on the amyloid substance of the organ. Instead of adopting Bernard's view, that normally, during life, glycogen passes as sugar into the hepatic venous blood, and thereby is conveyed to the lungs to be further disposed of, Pavy inclines to the belief that it may represent an intermediate stage in the formation of fat from materials absorbed from the alimentary canal.

Liver-sugar and Glycogen.—To demonstrate the presence of sugar in the liver, a portion of this organ, after being cut into small pieces, is bruised in a mortar to a pulp with a small quantity of water, and the pulp is boiled with sodium-sulphate in order to precipitate albuminous and colouring matters. The decoction is then filtered and may be tested for glucose (p. 284).

Glycogen ($C_6 H_{10} O_5$) is an amorphous, starch-like substance, odourless and tasteless, soluble in water, insoluble in alcohol. It is converted into glucose by boiling with dilute acids, or by contact with any animal ferment. It may be obtained by taking a portion of liver from a recently killed rabbit, and, after cutting it into small pieces, placing it for a short time in boiling water. It is then bruised in a mortar, until it forms a pulpy mass, and subsequently boiled in distilled water for about a quarter of an hour. The glycogen is precipitated from the filtered decoction by the addition of alcohol. Glycogen has been found in many other structures than the liver. (See Appendix.)

Glycosuria.—The facility with which the glycogen of the liver is transformed into sugar would lead to the expectation that this chemical change, under many circumstances, would occur to such an extent that sugar would be present not only in the hepatic veins, but in the blood generally, Such is frequently the case; the sugar when in excess in the blood being secreted by the kidneys, and thus appearing in variable quantities in the urine (Glycosuria).

Influence of the Nervous System in producing Glycosuria.—Glycosuria may be experimentally produced by puncture of the medulla oblongata in the region of the vaso-motor centre. The better fed the animal the larger is the amount of sugar found in the urine; whereas in the case of a starving animal no sugar appears. It is, therefore, highly probable that the sugar comes from the hepatic glycogen, since in the one case glycogen is in excess, and in the other it is almost absent. The nature of the influence is uncertain. It may be exercised in dilating the hepatic vessels, or possibly on the liver cells themselves. The whole course of the nervous stimulus cannot be traced to the liver, but at first it passes from the medulla down the spinal cord as far as —in rabbits—the fourth dorsal vertebra, and thence to the first thoracic ganglion.

Many other circumstances will cause glycosuria. It has been observed after the administration of various drugs, after the injection of urari, poisoning with carbonic oxide gas, the inhalation of ether, chloroform, etc., the injection of oxygenated blood into the portal venous system. It has been observed in man after injuries to the head, and in the course of various diseases.

The well-known disease, *diabetus mellitus*, in which a large quantity of sugar is persistently secreted daily with the urine, has, doubtless, some close relation to the normal glycogenic function of the liver; but the nature of the relationship is at present quite unknown.

The Intestinal Secretion, or **Succus Entericus.**—On account of the difficulty in isolating the secretion of the glands in the wall of the intestine (Brunner's and Lieberkühn's) from other secretions poured into the canal (gastric juice, bile, and pancreatic secretion), but little is known regarding the composition of the former fluid (intestinal juice, *succus entericus*).

It is said to be a yellowish alkaline fluid with a specific gravity of 1011, and to contain about 2·5 per cent. of solid matters (Thiry).

Functions.—The secretion of Brunner's glands is said to be able to convert proteids into peptones, and that of Lieberkühn's is believed to convert starch into sugar. To these functions of the *succus entericus* the powers of converting cane into grape sugar, and of turning cane sugar into lactic, and afterwards into butyric acid, are added by some physiologists. It also probably contains a milk-curdling ferment (W. Roberts).

The reaction which represents the conversion of cane sugar into grape sugar may be represented thus :—

$$\underset{\text{Saccharose}}{2\,C_{12}H_{22}O_{11}} + \underset{\text{Water}}{2\,H_2O} = \underset{\text{Dextrose}}{C_{12}H_{24}O_{12}} + \underset{\text{Lævulose}}{C_{12}H_{24}O_{12}}$$

The conversion is probably effected by means of a hydrolytic ferment. (Inversive ferment, Bernard.)

The *length and complexity* of the digestive tract seem to be closely connected with the character of the food on which an animal lives. Thus, in all carnivorous animals, such as the cat and dog, and pre-eminently in carnivorous birds, as hawks and herons, it is exceedingly short. The seals, which, though carnivorous, possess a very long intestine, appear to furnish an exception : but this is doubtless to be explained as an adaptation to their aquatic habits : their constant exposure to cold requiring that they should absorb as much as possible from their intestines.

Herbivorous animals, on the other hand, and the ruminants especially, have very long intestines (in the sheep 30 times the length of the body) which is no doubt to be connected with their lowly nutritious diet. In others, such as the rabbit, though the intestines are not excessively long, this is compensated by the great length and capacity of the cæcum. In man, the length of the intestines is intermediate between the extremes of the carnivora and herbivora, and his diet also is intermediate.

Summary of the Digestive Changes in the Small Intestine.

In order to understand the changes in the food which occur during its passage through the small intestine, it will be well to refer briefly to the state in which it leaves the stomach through the pylorus. It has been said before, that the chief office of the stomach is not only to mix into an uniform mass all the varieties of food that reach it through the œsophagus, but especially to dissolve the nitrogenous portion by means of the gastric juice. The fatty matters, during their sojourn in the stomach, become more thoroughly mingled with the other constituents of the food taken, but are not yet in a state fit for absorption. The conversion of starch into sugar, which began in the mouth, has been interfered with, if not altogether stopped. The soluble matters—both those which were so from the first, as sugar and saline matter, and the gastric peptones—have begun to disappear by absorption into the blood-vessels, and the same thing has befallen such fluids as may have been swallowed,—wine, water, etc.

The thin pultaceous chyme, therefore, which during the whole period of gastric digestion, is being constantly squeezed or strained through the pyloric orifice into the duodenum, consists of albuminous matter, broken down, dissolving and half dissolved; fatty matter broken down and melted, but not dissolved at all; starch very slowly in process of conversion into sugar, and as it becomes sugar, also dissolving in the fluids with which it is mixed; while, with these are mingled gastric fluid, and fluid that has been swallowed, together with such portions of the food as are not digestible, and will be finally expelled as part of the fæces.

On the entrance of the chyme into the duodenum, it is subjected to the influence of the bile and pancreatic juice, which are then poured out, and also to that of the succus entericus. All these secretions have a more or less alkaline reaction, and by their admixture with the gastric chyme, its acidity becomes less and less until at length, at about the middle of the small intestine, the reaction becomes alkaline and continues so as far as the ileo-cæcal valve.

The special digestive functions of the small intestine may be taken in the following order:—

(1.) One important duty of the small intestine is the alteration of the *fat* in such a manner as to make it fit for absorption; and there is no doubt that this change is chiefly effected in the upper part of the small intestine. What is the exact share of the process, however, allotted respectively to the bile, to the pancreatic secretion, and to the intestinal juice, is still uncertain,—probably the pancreatic juice is the most important. The fat is changed in two ways. (*a*). To a slight extent it is chemically decomposed by the alkaline secretions with which it is mingled, and a soap is the result. (*b*). It is emulsionised, *i.e.*, its particles are minutely subdivided and diffused, so that the mixture assumes the condition of a milky fluid, or emulsion. As will be seen in the next Chapter, most of the fat is absorbed by the lacteals of the intestine, but a small part, which is saponified, is also absorbed by the blood-vessels.

(2.) The *albuminous* substances which have been partly dissolved in the stomach, and have not been absorbed, are subjected to the action of the pancreatic and intestinal secretions. The pepsin is rendered inert by being precipitated together with the gastric peptones and parapeptones, as soon as the chyme meets with bile. By these means the pancreatic ferment trypsin is enabled to proceed with the further conversion of the parapeptones into peptones, and of part of the peptones (hemipeptone, Kühne) into leucin and tyrosin. *Albuminous* substances, which are chemically altered in the process of digestion (peptones), and gelatinous matters similarly changed, are absorbed by both the blood-vessels and lymphatics of the intestinal mucous membrane. Albuminous matters, in a state of solution, which have not undergone the peptonic change, are probably, from the difficulty with which they *diffuse*, absorbed, if at all, almost solely by the lymphatics.

(3.) The *starchy*, or amyloid portions of the food, the conversion of which into dextrin and sugar was more or less interrupted during its stay in the stomach, is now acted on briskly by the pancreatic juice and the succus entericus; and the sugar, as it is formed, is dissolved in the intestinal fluids, and is absorbed chiefly by the blood-vessels.

(4.) *Saline* and *saccharine* matters, as common salt, or cane sugar, if not in a state of solution beforehand in the saliva or other fluids which may have been swallowed with them, are at once dissolved in the stomach, and if not here absorbed, are soon taken up in the small intestine; the blood-vessels, as in the last case, being chiefly concerned in the absorption. Cane sugar is in part or wholly converted into grape-sugar before its absorption. This is accomplished partially in the stomach, but also by a ferment in the succus entericus.

(5.) The *liquids*, including in this term the ordinary drinks, as water, wine, ale, tea, etc., which may have escaped absorption in the stomach, are absorbed probably very soon after their entrance into the intestine; the fluidity of the contents of the latter being preserved more by the constant secretion of fluid by the intestinal glands, pancreas, and liver, than by any given portion of fluid, whether swallowed or secreted, remaining long unabsorbed. From this fact, therefore, it may be gathered that there is a kind of circulation constantly proceeding from the intestines into the blood, and from the blood into the intestines again; for as all the fluid—a very large amount—secreted by the intestinal glands, must come from the blood, the latter would be too much drained, were it not that the same fluid after secretion is again re-absorbed into the current of blood—going into the blood charged with nutrient products of digestion—coming out again by secretion through the glands in a comparatively uncharged condition.

At the lower end of the small intestine, the chyme, still thin and pultaceous, is of a light yellow colour, and has a distinctly fæcal odour. This odour depends upon the formation of indol. In this state it passes through the ileo-cæcal opening into the large intestine.

Summary of the Digestive Changes in the Large Intestine.

The changes which take place in the chyme in the *large* intestine are probably only the continuation of the same changes that occur in the course of the food's passage through the upper part of the intestinal canal. From the absence of villi, however, we may conclude that absorption, especially of fatty matter, is in great part completed in the small intestine; while, from the still half-liquid, pultaceous consistence of the chyme when it first enters the cæcum, there can be no doubt that the absorption of liquid is not by any means concluded. The peculiar odour, moreover, which is acquired after a short time by the contents of the large bowel, would seem to indicate a further chemical change in the alimentary matters or in the digestive fluids, or both. The acid reaction, which had disappeared in the small bowel, again becomes very manifest in the cæcum—probably from acid fermentation-processes in some of the materials of the food.

There seems no reason to conclude that any special 'secondary digestive' process occurs in the cæcum or in any other part of the large intestine. Probably any constituent of the food which has escaped digestion and absorption in the small bowel may be digested in the large intestine; and the power of this part of the intestinal canal to digest fatty, albuminous, or other matters, may be gathered from the good effects of nutrient enemata, so frequently given when from any cause there is difficulty in introducing food into the stomach. In ordinary healthy digestion, however, the changes which ensue in the chyme after its passage into the large intestine, are mainly the absorption of the more liquid parts, and the completion of the changes which were proceeding in the small intestine,—the process being assisted by the secretion of the numerous tubular glands therein present.

Fæces.—By these means the contents of the large intestine, as they proceed towards the rectum, become more and more solid, and losing their more liquid and nutrient parts, gradually acquire the odour and consistence characteristic of *fæces*. After a sojourn of uncertain duration in the sigmoid flexure of the colon, or in the rectum, they are finally expelled by the act of defæcation.

The average quantity of solid fæcal matter evacuated by the human adult in twenty-four hours is about six or eight ounces.

Composition of Fæces.

Water	733·00
Solids	267·00
Special excrementitious oonstituents :—Excretin, excretoleic acid (Marcet), and stercorin (Austin Flint).	267·00
Salts :—Chiefly phosphate of magnesium and phosphate of calcium, with small quantities of iron, soda, lime, and silica.	
Insoluble residue of the food (chiefly starch grains, woody tissue, particles of cartilage and fibrous tissue, undigested muscular fibres or fat, and the like, with insoluble substances accidentally introduced with the food.	
Mucus, epithelium, altered colouring matter of bile, fatty acids, etc.	
Varying quantities of other constituents of bile, and derivatives from them.	

Length of Intestinal Digestive Period.—The time occupied by the journey of a given portion of food from the stomach to the anus, varies considerably even in health, and on this account, probably, it is that such different opinions have been expressed in regard to the subject. About twelve hours are occupied by the journey of an ordinary meal through the *small* intestine, and twenty-four to thirty-six hours by the passage through the *large* bowel. (Brinton.)

Defæcation.—Immediately before the act of voluntary expulsion of fæces (*defæcation*) there is usually, first an inspiration, as in the case of coughing, sneezing, and vomiting; the glottis is then closed, and the diaphragm fixed. The abdominal muscles are contracted as in expiration; but as the glottis is closed, the whole of their pressure is exercised on the abdominal contents. The sphincter of the rectum being relaxed, the evacuation of its contents takes place accordingly; the effect being, of course, increased by the peristaltic action of the intestine. As in the other actions just referred to, there is as much tendency to the escape of the contents of the lungs or stomach as of the rectum; but the pressure is relieved only at the orifice, the sphincter of which instinctively or involuntarily yields (see fig. 144).

Nervous Mechanism of Defæcation.—The anal sphincter muscle is normally in a state of tonic contraction. The nervous centre which governs this contraction is probably situated in the lumbar region of the spinal cord, inasmuch as in cases of division of the cord above this region the sphincter regains, after a time, to some extent the tonicity which is lost immediately after the operation. By an effort of the will, acting through the centre, the contraction may be relaxed or increased. In ordinary cases the apparatus is set in action by the gradual accumulation of fæces in the sigmoid flexure and rectum pressing against the sphincter and causing its relaxation; this sensory impulse acting through the brain and reflexly through the spinal centre. Peristaltic action, especially of the sigmoid flexure in pressing onwards the fæces against the sphincter, is a very important part of the act.

The Gases contained in the Stomach and Intestines.—Under ordinary circumstances, the alimentary canal contains a considerable quantity of gaseous matter. Any one who has had occasion, in a post-mortem examination, either to lay open the intestines, or to let out the gas which they contain, must have been struck by the small space afterwards occupied by the bowels, and by the large degree, therefore, in which the gas, which naturally distends them, contributes to fill the cavity of the abdomen. Indeed, the presence of air in the intestines is so constant, and, within certain limits, the amount in health so uniform, that there can be no doubt that its existence here is not a mere accident, but intended to serve a definite and important purpose, although, probably, a mechanical one.

Sources.—The sources of the gas contained in the stomach and bowels may be thus enumerated :—

1. Air introduced in the act of swallowing either food or saliva ; 2. Gases developed by the decomposition of alimentary matter or of the secretions and excretions mingled with it in the stomach and intestines ; 3. It is probable that a certain mutual interchange occurs between the gases contained in the alimentary canal, and those present in the blood of these gastric and intestinal blood-vessels ; but the conditions of the exchange are not known, and it is very doubtful whether anything like a true and definite secretion of gas from the blood into the intestines or stomach ever takes place. There can be no doubt, however, that the intestines may be the proper excretory organs for many odorous and other substances, either absorbed from the air taken into the lungs in inspiration, or absorbed in the upper part of the alimentary canal, again to be excreted at a portion of the same tract lower down—in either case assuming rapidly a gaseous form after their excretion, and in this way, perhaps, obtaining a more ready egress from the body. It is probable that, under ordinary circumstances, the gases of the stomach and intestines are derived chiefly from the second of the sources which have been enumerated (Brinton).

Composition of Gases contained in the Alimentary Canal.

(TABULATED FROM VARIOUS AUTHORITIES BY BRINTON.)

Whence obtained.	Composition by Volume.					
	Oxygen.	Nitrog.	Carbon. Acid.	Hydrog.	Carburet. Hydrogen.	Sulphuret. Hydrogen.
Stomach	11	71	14	4	—	—
Small Intestines	—	32	30	38	—	trace.
Cæcum	—	66	12	8	13	
Colon	—	35	57	6	8	
Rectum	—	46	43	—	11	
Expelled *per anum*	—	22	41	19	19	½

Movements of the Intestines.—It remains only to consider the manner in which the food and the several secretions mingled with it are moved through the intestinal canal, so as to be slowly subjected to the influence of fresh portions of intestinal secretion, and as slowly exposed to the absorbent power of all the villi and blood vessels of the mucous membrane. The movement of the intestines is *peristaltic* or *vermicular*, and is effected by the alternate contractions and dilatations of successive portions of the intestinal coats. The contractions, which may commence at any point of the intestine, extend in a wave-like manner along the tube. In any given portion, the longitudinal muscular fibres contract first, or more than the circular; they draw a portion of the intestine upwards, or, as it were, backwards, over the substance to be propelled, and then the circular fibres of the same portion contracting in succession from above downwards, or, as it were, from behind forwards, press on the substance into the portion next below, in which at once the same succession of action next ensues. These movements take place slowly and, in health, are commonly unperceived by the mind; but they are perceptible when they are accelerated under the influence of any irritant.

The movements of the intestines are sometimes retrograde; and there is no hindrance to the backward movement of the contents of the small intestine. But almost complete security is afforded against the passage of the contents of the large into the small intestine by the ileo-cæcal valve. Besides,—the orifice of communication between the ileum and cæcum (at the borders of which orifice are the folds of mucous membrane which form the valve) is encircled with muscular fibres, the contraction of which prevents the undue dilatation of the orifice.

Proceeding from above downwards, the muscular fibres of the large intestine become, on the whole, stronger in direct proportion to the greater strength required for the onward moving of the fæces, which are gradually becoming firmer. The greatest strength is in the rectum, at the termination of which the circular unstriped muscular fibres form a strong band called the *internal* sphincter; while an *external* sphincter muscle with striped fibres is placed rather lower down, and more externally, and as we have seen above, holds the orifice close by a constant slight tonic contraction.

Experimental irritation of the brain or cord produces no evident or constant effect on the movements of the intestines during life; yet in consequence of certain conditions of the mind the movements are accelerated or retarded; and in paraplegia the intestines appear after a time much weakened in their power, and costiveness, with a tympanitic condition, ensues. Immediately after death, irritation of both the sympathetic and pneumo-gastric nerves, if not too strong, induces genuine peristaltic movements of the intestines. Violent irritation stops the movements. These stimuli act, no doubt, not directly on the muscular tissue of the intestine, but on the ganglionic plexus before referred to.

Influence of the Nervous System on Intestinal Digestion. —As in the case of the œsophagus and stomach, the peristaltic movements of the intestines are directly due to reflex action through the ganglia and nerve fibres distributed so abundantly in their walls (p. 315); the presence of chyme acting as the stimulus, and few or no movements occurring when the intestines are empty. The intestines are, moreover, connected with the higher nerve-centres by the splanchnic nerves, as well as other branches of the sympathetic which come to them from the cœliac and other abdominal plexuses.

The splanchnic nerves are in relation to the intestinal movements, *inhibitory*—these movements being retarded or stopped when the splanchnics are irritated. As the vasomotor nerves of the intestines, the splanchnics are also much concerned in intestinal digestion.

CHAPTER IX.

ABSORPTION.

The process of Absorption has, for one of its objects, the introduction into the blood of fresh materials from the food and air and of whatever comes into contact with the external or internal surfaces of the body; and, for another, the gradual removal of parts of the body itself, when they need to be renewed. In both these offices, *i.e.*, in both absorption from without and absorption from within, the process manifests some variety, and a very wide range of action; and in both two sets of vessels are, or may be, concerned, namely, the *Blood-vessels*, and the Lymph-vessels or *Lymphatics* to which the term Absorbents has been also applied.

The Lymphatic Vessels and Glands.

Distribution.—The principal vessels of the lymphatic system are, in structure and general appearance, like very small and thin-walled veins, and like them are provided with valves. By one extremity they commence by fine microscopic branches, the *lymphatic capillaries* or *lymph-capillaries*, in the organs and tissues of the body, and by their other extremities they end directly or indirectly in two trunks which open into the large veins near the heart (fig. 206). Their contents, the *lymph* and *chyle*, unlike the blood, pass only in one direction, namely, from the fine branches to the trunk and so to the large veins, on entering which they are mingled with the stream of blood, and form part of its constituents. Remembering the course of the fluid in the lymphatic vessels, viz., its passage in the direction only *towards* the large veins in the neighbourhood of the heart, it will readily be seen from fig. 206 that the greater part of the contents of the lymphatic system of vessels passes through a comparatively large trunk called the *thoracic duct*, which finally empties its contents into the blood-stream, at the junction of the internal jugular and subclavian veins of the left side. There is a smaller duct on the right side. The lymphatic vessels of the intestinal canal are called *lacteals*, because, during digestion, the fluid contained in them resembles milk in appearance; and the *lymph* in the lacteals during the period of digestion is called *chyle*. There is no essential distinction, however, between lacteals and lymphatics. In some parts of their course all lymphatic vessels pass through certain bodies called *lymphatic glands.*

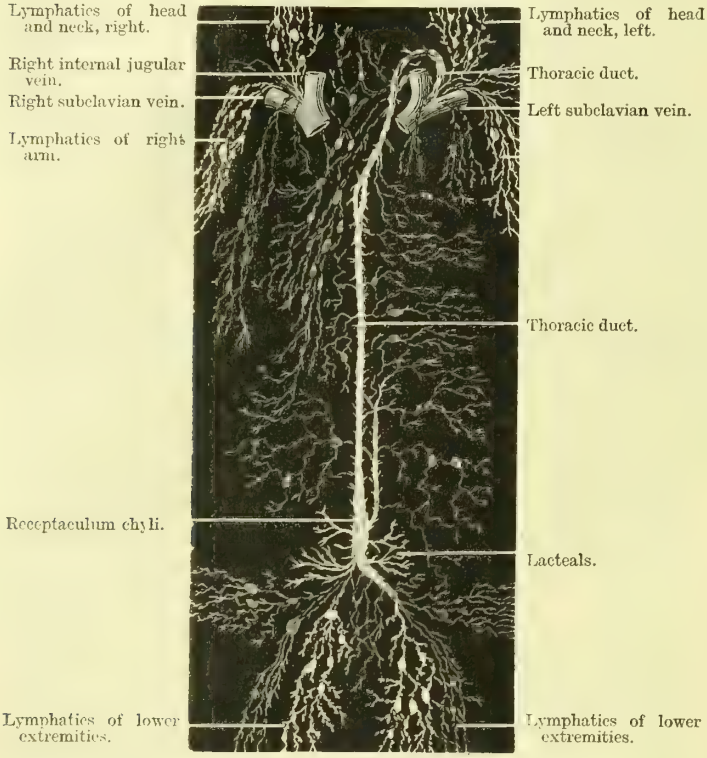
Lymphatics of head and neck, right.
Lymphatics of head and neck, left.
Right internal jugular vein.
Thoracic duct.
Right subclavian vein.
Left subclavian vein.
Lymphatics of right arm.
Thoracic duct.
Receptaculum chyli.
Lacteals.
Lymphatics of lower extremities.
Lymphatics of lower extremities.

Fig. 206.—*Diagram of the principal groups of lymphatic vessels* (from Quain).

Lymphatic vessels are distributed in nearly all parts of the body. Their existence, however, has not yet been determined in the placenta, the umbilical cord, the membranes of the ovum, or in any of the non-vascular parts, as the nails, cuticle, hair and the like.

Origin of Lymph Capillaries.—The lymphatic *capillaries* commence most commonly either in closely-meshed networks, or in irregular lacunar spaces between the various structures of which the different organs are composed. Such irregular spaces, forming what is now termed the *lymph-canalicular system*, have been shown to exist in many tissues. In serous membranes such as the omentum and mesentery they occur as a connected system of very irregular branched spaces partly occupied by connective tissue-corpuscles, and both in these and in many other tissues are found to communicate freely with regular lymphatic vessels. In many cases, though they are formed mostly by the chinks and crannies between the blood-vessels, secreting ducts, and other parts which may happen to form the framework of the organ in which they exist, they are lined by a distinct layer of endothelium.

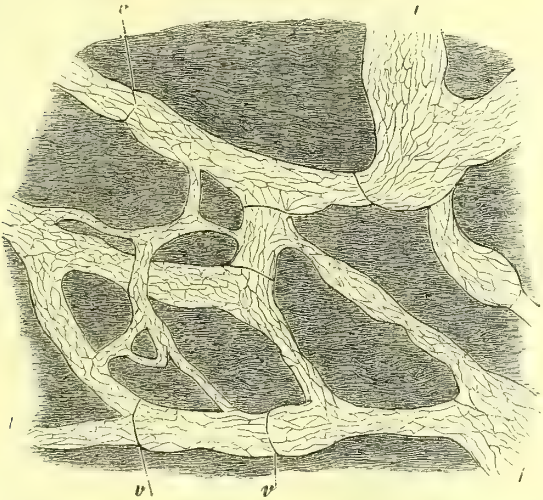

Fig. 207.—*Lymphatics of central tendon of rabbit's diaphragm*, stained with silver nitrate. The ground substance has been shaded diagrammatically to bring out the lymphatics clearly. *l.* Lymphatics lined by long narrow endothelial cells, and showing *v.* valves at frequent intervals (Schofield).

The lacteals offer an illustration of another mode of origin, namely, in blind dilated extremities (figs. 192 and 193); but there is no essential difference in structure between these and the lymphatic capillaries of other parts.

Structure of Lymph Capillaries.—The structure of lymphatic capillaries is very similar to that of blood-capillaries: their walls consist of a single layer of endothelial cells of an elongated form and sinuous outline, which cohere along their edges to form a delicate membrane. They differ from blood capillaries mainly in their larger and very variable calibre, and in their numerous communications with the spaces of the lymph-canalicular system.

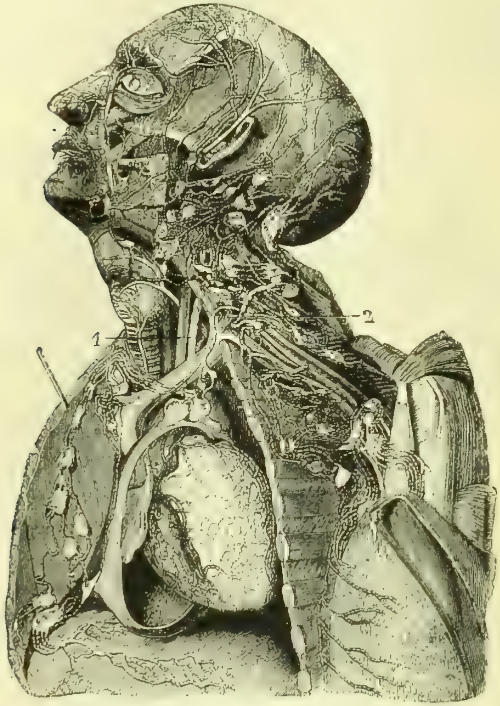

Fig. 208.—*Lymphatic vessels of the head and neck and the upper part of the trunk* (Mascagni). $\frac{1}{8}$.—The chest and pericardium have been opened on the left side, and the left mamma detached and thrown outwards over the left arm, so as to expose a great part of its deep surface. The principal lymphatic vessels and glands are shown on the side of the head and face, and in the neck, axilla, and mediastinum. Between the left internal jugular vein and the common carotid artery, the upper ascending part of the thoracic duct marked 1, and above this, and descending to 2, the arch and last part of the duct. The termination of the upper lymphatics of the diaphragm in the mediastinal glands, as well as the cardiac and the deep mammary lymphatics, is also shown.

Communications of the Lymphatics.—The fluid part of the blood constantly exudes or is strained through the walls of the blood-capillaries, so as to moisten all the surrounding tissues, and occupies the interspaces which exist among their different

Fig. 209.

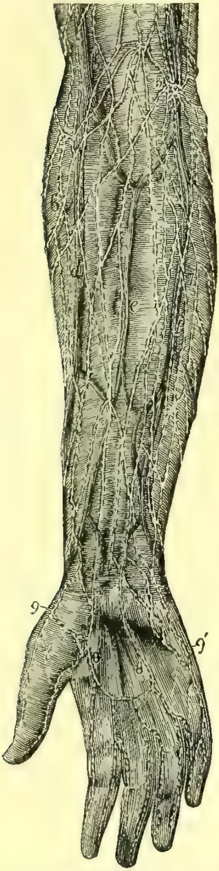

Fig. 210.

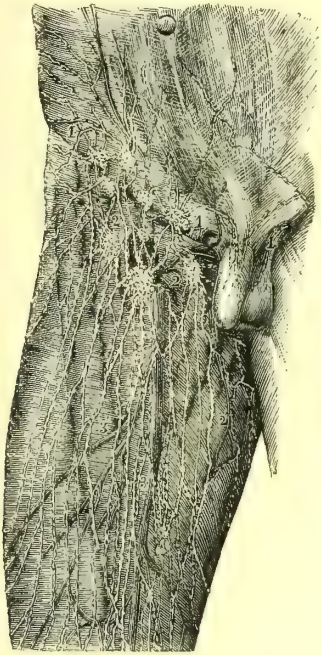

Fig. 209.—*Superficial lymphatics of the forearm and palm of the hand*, $\frac{1}{4}$. 5. Two small glands at the bend of the arm. 6. Radial lymphatic vessels. 7. Ulnar lymphatic vessels. 8, 8. Palmar arch of lymphatics. 9, 9′. Outer and inner sets of vessels. *b*. Cephalic vein. *d*. Radial vein. *e*. Median vein. *f*. Ulnar vein. The lymphatics are represented as lying on the deep fascia. (Mascagni.)

Fig. 210.—*Superficial lymphatics of right groin and upper part of thigh*, $\frac{1}{6}$. 1. Upper inguinal glands. 2, 2′. Lower inguinal or femoral glands. 3, 3′. Plexus of lymphatics in the course of the long saphenous vein. (Mascagni.)

elements. These same interspaces have been shown, as just stated, to form the beginnings of the lymph-capillaries ; and the latter, therefore, are the means of collecting the exuded blood plasma, and returning that part which is not directly absorbed by the tissues into the blood-stream. For many years, the notion of the existence of any such channels between the blood-vessels and lymph-vessels as would admit blood-corpuscles, has been given up; observations having proved that, for the passage of such corpuscles, it is not necessary to assume the presence of any special channels at all, inasmuch as blood-corpuscles can pass bodily, without much difficulty, through the walls of the blood-capillaries and small veins (p. 199), and could pass with still less trouble, probably, through the comparatively ill-defined walls of the capillaries which contain lymph.

It is worthy of note that, in many animals, both arteries and veins, especially the latter, are often found to be more or less completely ensheathed in large lymphatic channels. In turtles, crocodiles, and many other animals, the abdominal aorta is enclosed in a large lymphatic vessel.

Stomata.—In certain parts of the body openings exist by which lymphatic capillaries directly communicate with parts hitherto supposed to be closed cavities. If the peritoneal cavity be injected with milk, an injection is obtained of the plexus of lymphatic vessels of the central tendon of the diaphragm (fig. 207); and on removing a small portion of the central tendon, with its peritoneal surface uninjured, and examining the process of absorption under the microscope, the milk-globules run towards small natural openings or *stomata* between the epithelial cells, and disappear by passing vortex-like through them. The *stomata*, which have a roundish outline, are only wide enough to admit two or three milk-globules abreast, and never exceed the size of an epithelial cell.

Pseudostomata.—When absorption into the lymphatic system takes place in membranes covered by epithelium or endothelium through the interstitial or intercellular cement-substance, it is said to take place through *pseudostomata.*

Demonstration of Lymphatics of Diaphragm.—The stomata on the peritoneal surface of the diaphragm are the openings of short vertical canals which lead up into the lymphatics, and are lined by cells like those of germinating endothelium (p. 27). By introducing a solution of Berlin blue into the peritoneal cavity of an animal shortly after death, and suspending it, head downwards, an injection of the lymphatic vessels of the diaphragm, through the stomata on its peritoneal surface, may readily be obtained, if artificial respiration be carried on for about half an hour. In this way it has been found that in the rabbit the lymphatics are arranged between the tendon bundles of the centrum tendineum; and they are hence termed *interfascicular.* The centrum tendineum is coated by endothelium on its pleural and peritoneal surfaces, and its substance consists of tendon bundles arranged in concentric rings towards the pleural side and in radiating bundles towards the peritoneal side.

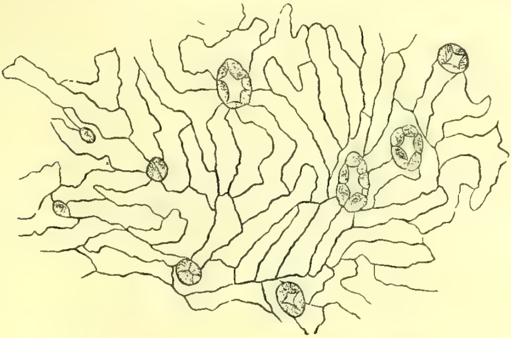

Fig. 211.—*Peritoneal surface of septum cisternæ lymphaticæ magnæ of frog.* The stomata, some of which are open, some collapsed, are surrounded by germinating endothelium. × 160. (Klein.)

The lymphatics of the anterior half of the diaphragm open into those of the anterior mediastinum, while those of the posterior half pass into a lymphatic vessel in the posterior mediastinum, which soon enters the thoracic duct. Both these sets of vessels, and the glands into which they pass, are readily injected by the method above described; and there can be little doubt that during life the flow of lymph along these channels is chiefly caused by the action of the diaphragm during respiration. As it descends in inspiration, the spaces between the *radiating* tendon bundles dilate, and lymph is sucked from the peritoneal cavity, through the widely open stomata, into the interfascicular lymphatics. During expiration, the spaces between the *concentric* tendon bundles dilate, and the lymph is squeezed into the lymphatics towards the pleural surface. (Klein.) It thus appears probable that during health there is a continued sucking in of lymph from the peritoneum into the lymphatics by the "pumping" action of the diaphragm; and there is doubtless an equally continuous exudation of fluid from the general serous surface of the peritoneum. When this balance of transudation and absorption is disturbed, either by increased transudation or some impediment to absorption, an accumulation of fluid necessarily takes place (ascites).

Stomata have been found in the pleura; and as they may be presumed to exist in other serous membranes, it would seem as if the serous cavities, hitherto supposed closed, form but a large lymph-sinus or widening out, so to speak, of the lymph-capillary system with which they directly communicate.

Structure of Lymphatic Vessels.—The larger vessels are very like veins, having an external coat of fibro-cellular tissue, with elastic filaments; within this, a thin layer of fibro-cellular tissue, with plain muscular fibres, which have, principally, a circular direction, and are much more abundant in the small than in the larger vessels; and again, within this, an inner elastic layer of longitudinal fibres, and a lining of epithelium; and numerous valves. The valves, constructed like those of veins, and with the free edges turned towards the heart, are usually arranged in pairs, and, in the small vessels, are so closely placed, that when the vessels are full, the valves constricting them where their edges are attached, give them a peculiar beaded or knotted appearance.

Current of the Lymph.—With the help of the valvular mechanism (1) all occasional pressure on the exterior of the lymphatic and lacteal vessels propels the lymph towards the heart: thus muscular and other external pressure accelerates the flow of the lymph as it does that of the blood in the veins. The actions of (2) the muscular fibres of the small intestine, and probably the layer of organic muscle present in each intestinal villus, seem to assist in propelling the chyle: for, in the small intestine of a mouse, the chyle has been seen moving with intermittent propulsions that appeared to correspond with the peristaltic movements of the intestine. But for the general propulsion of the lymph and chyle, it is probable that, together with (3) the *vis a tergo* resulting from absorption (as in the ascent of sap in a tree), and from external pressure, some of the force may be derived (4) from the contractility of the vessel's own walls. The respiratory movements, also, (5) favour the current of lymph through the thoracic duct as they do the current of blood in the thoracic veins (p. 253).

Lymphatic Glands are small round or oval compact bodies varying in size from a hempseed to a bean, interposed in the course of the lymphatic vessels, and through which the chief part of the lymph passes in its course to be discharged into the blood vessels. They are found in great numbers in the mesentery, and along the great vessels of the abdomen, thorax, and neck; in the axilla and groin; a few in the popliteal space, but not further down the leg, and in the arm as far as the elbow.

Some lymphatics do not, however, pass through glands before entering the thoracic duct.

Structure.—A lymphatic gland is covered externally by a capsule of connective tissue, generally containing some unstriped muscle. At the inner side of the gland, which is somewhat concave (*hilus*) (fig. 212, *a*), the capsule sends processes inwards in which the blood vessels are contained, and these join with other processes called *trabeculæ* (fig. 215, *t.r.*) prolonged from the inner surface of the part of the capsule covering the convex or outer part of the gland; they have a structure similar to that of the capsule, and entering the gland from all sides, and freely communicating, form a fibrous supporting *stroma.* The interior of the gland is seen on section, even when examined with the naked eye, to be made up of two parts, an outer or *cortical* (fig. 212, *c*, *c*), which is light coloured, and an inner of redder appearance, the *medullary* portion (fig. 212). In the outer or cortical part of the gland (fig. 215, *c*) the intervals between the trabeculæ are comparatively large and more or less triangular, the intercommunicating spaces being termed *alveoli;* whilst in the more central or medullary part a finer meshwork is formed by the more free anastomosis of the trabecular processes. In the alveoli of the cortex and in the meshwork formed by the trabeculæ in the medulla, is contained the proper gland structure. In the former it is arranged as follows (fig. 215): occupying the central and chief part of each alveolus, is a more or less wedge-shaped mass (*l.h.*) of adenoid tissue, densely packed with lymph corpuscles; but at the periphery surrounding the central portion and immediately next the capsule and trabeculæ, is a more open meshwork of adenoid tissue constituting the

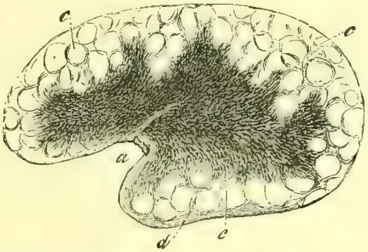

Fig. 212.—*Section of a mesenteric gland from the ox,* slightly magnified. *a*, Hilus; *b* (in the central part of the figure), medullary substance; *c*, cortical substance with indistinct alveoli; *d*, capsule (Kölliker).

lymph sinus or *channel* (*l.s.*), and containing fewer lymph corpuscles; The central mass is enclosed in endothelium, the cells of which

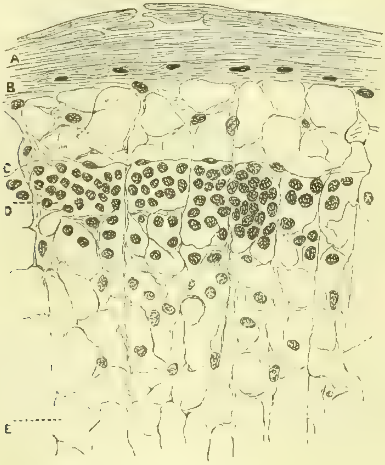

Fig. 213.—*From a vertical section through the capsule, cortical sinus and peripheral portion of follicle of a human compound lymphatic gland.* The section had been shaken, so as to get rid of most of the lymph corpuscles. A. Outer stratum of capsule, consisting of bundles of fibrous tissue cut at various angles. B. Inner stratum, showing fibres of connective tissue with nuclei of flattened connective-tissue corpuscles. Beneath this (between B and C) is the lymph-sinus or lymph-path, containing a reticulum coated by flat nucleated endothelial cells. C. Fine nucleated endothelial membrane, marking boundary of the lymph-follicle. The rest of the section from C to E is the adenoid tissue of the lymph-follicle, which consists of a fine reticulum, E, with numerous lymph corpusles, D. They are so closely packed that the adenoid reticulum is invisible till the section has been shaken so as to dislodge a number of the lymph-corpuscles × 350 (Klein and Noble Smith).

join by their processes, the processes of the adenoid framework of the lymph sinus. The trabeculæ are also covered with endothelium. The lining of the central mass does not prevent the passage of fluids and even of corpuscles into the lymph sinus. The framework of the adenoid tissue of the lymph sinus is nucleated, that of the central mass is non-nucleated. At the inner part of the alveolus, the wedge-shaped central mass bifurcates (fig. 215) or divides into two or more smaller rounded or cord-like masses and here joining with those from the other alveoli, form a much closer arrangement of the gland tissue (fig. 214, *a*) than in the cortex; spaces (fig. 214, *b*), are left within those anastomosing cords, in which are found portions of the trabecular meshwork and the continuation of the lymph sinus (*b*, *c*).

The essential structure of lymphatic-gland substance resembles that which was described as existing, in a simple

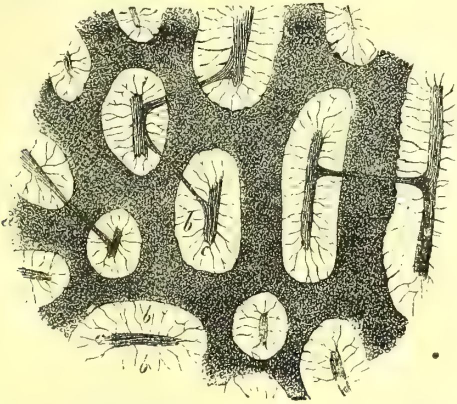

Fig. 214.—*Section of medullary substance of an inguinal gland of an ox*; *a*, *a*, glandular substance or pulp forming rounded cords joining in a continuous net (dark in the figure); *c. c*, trabeculæ; the space, *b*, *b*, between these and the glandular substance is the lymph-sinus, washed clear of corpuscles and traversed by filaments of retiform connective-tissue × 90 (Kölliker).

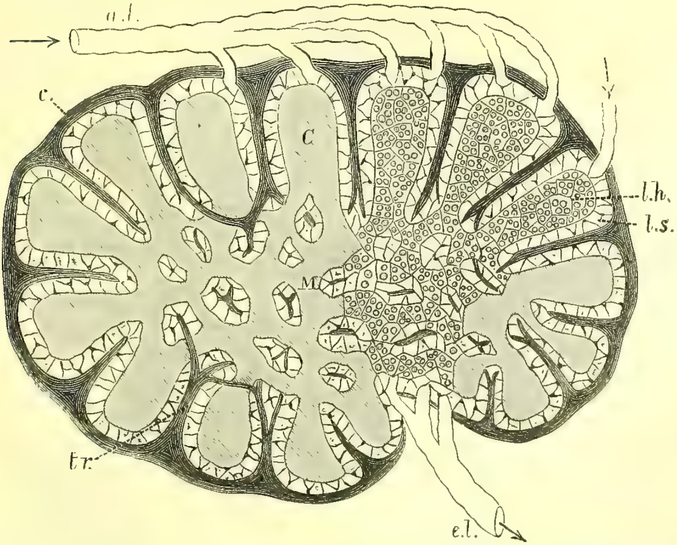

Fig. 215.—*Diagrammatic section of Lymphatic gland.* *a. l.*, Afferent; *e. l.* efferent lymphatics; *C*, cortical substance; *l. h.*, reticulating cords of medullary substance; *l. s.*, lymph-sinus; *c.*, fibrous coat sending in trabeculæ; *t. r.*, into the substance of the gland (Sharpey).

form, in the interior of the solitary and agminated intestinal follicles.

The lymph enters the gland by several afferent vessels (fig. 215, *a.l.*) which open beneath the capsule into the lymph-channel or lymph-path; at the same time they lay aside all their coats except the endothelial lining, which is continuous with the lining of the lymph-path. The *efferent* vessels (fig. 215, *e.l.*) begin in the medullary part of the gland, and are continuous with the lymph-path here as the afferent vessels were with the cortical portion; the endothelium of one is continuous with that of the other.

The efferent vessels leave the gland at the *hilus*, the more or less concave inner side of the gland, and generally either at once or very soon after join together to form a single vessel.

Blood-vessels which enter and leave the gland at the hilus are freely distributed to the trabecular tissue and to the gland-pulp (fig. 216).

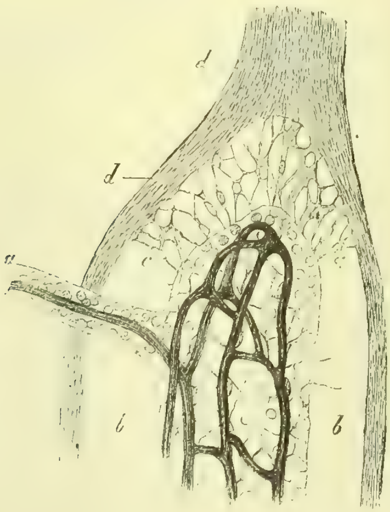

Fig. 216.—*A small portion of medullary substance from a mesenteric gland of the ox, d, d,* trabeculæ; *a*, part of a cord of glandular substances from which all but a few of the lymph-corpuscles have been washed out to show its supporting meshwork of retiform tissue and its capillary blood-vessels (which have been injected, and are dark in the figure); *b*, *b*, lymph-sinus, of which the retiform tissue is represented only at *c*, *c*. × 300 (Kölliker).

The tonsils, in part, and Peyer's glands of the intestine, are really lymphatic glands, and doubtless discharge similar functions.

The Lymph and Chyle.

The *lymph*, contained in the lymphatic vessels, is, under ordinary circumstances, a clear, transparent, and yellowish fluid. It is devoid of smell, is slightly alkaline, and has a saline taste. As seen with the microscope in the small transparent vessels of the tail of the tadpole, it usually contains no corpuscles or particles of any kind; and it is only in the larger trunks in which any corpuscles are to be found. These corpuscles are similar to colourless blood-corpuscles. The fluid in which the corpuscles float is albuminous, and contains no fatty particles or molecular base; but is liable to variations according to the general state of the blood, and to that of the organ from which the lymph is derived. As it advances towards the thoracic duct, and after passing through the lymphatic glands, it becomes spontaneously coagulable and the number of corpuscles is much increased. The fluid contained in the lacteals is clear and transparent during fasting, and differs in no respect from ordinary lymph; but, during digestion, it becomes milky, and is termed *chyle.*

Chyle is an opaque, whitish, milky fluid, neutral or slightly alkaline in reaction. Its whiteness and opacity are due to the presence of innumerable particles of oily or fatty matter, of exceedingly minute though nearly uniform size, measuring on the average about $\frac{1}{30000}$ of an inch. These constitute what is termed the *molecular base* of chyle. Their number, and consequently the opacity of the chyle, are dependent upon the quantity of fatty matter contained in the food. The fatty nature of the molecules is made manifest by their solubility in ether, and, when the ether evaporates, by their being deposited in various-sized drops of oil. Each molecule probably consists of oil coated over with albumen, in the manner in which oil always becomes covered when set free in minute drops in an albuminous solution. This is proved when water or dilute acetic acid is added to chyle, many of the molecules are lost sight of, and oil-drops appear in their place, as the investments of the molecules have been dissolved, and their oily contents have run together.

Except these molecules, the chyle taken from the villi or from lacteals near them, contains no other solid or organised bodies. The fluid in which the molecules float is albuminous, and does not spontaneously coagulate. But as the chyle passes on towards the thoracic duct, and especially while it traverses one or more of the mesenteric glands, it is elaborated. The quantity of molecules and oily particles gradually diminishes; cells, to which the name of *chyle-corpuscles* is given, are developed in it; and it acquires the property of coagulating spontaneously. The higher in the thoracic duct the chyle advances, the more is it, in all these respects, developed; the greater is the number of chyle-corpuscles, and the larger and firmer is the clot which forms in it when withdrawn and left at rest. Such a clot is like one of blood without the red corpuscles, having the chyle corpuscles entangled in it, and the fatty matter forming a white creamy film on the surface of the serum. But the clot of chyle is softer and moister than that of blood. Like blood, also, the chyle often remains for a long time in its vessels without coagulating, but coagulates rapidly on being removed from them. The existence of the materials which, by their union form fibrin, is, therefore, certain; and their increase appears to be commensurate with that of the corpuscles.

The structure of the chyle-corpuscles was described when speaking of the white corpuscles of the blood, with which they are identical.

Chemical Composition of Lymph and Chyle.—From what has been said, it will appear that perfect chyle and lymph are, in essential characters, nearly similar, and scarcely differ, except in the preponderance of fatty and proteid matter in the chyle.

Chemical Composition of Lymph and Chyle (Owen Rees).

	I. Lymph (Donkey).	II. Chyle (Donkey).	III. Mixed Lymph & Chyle (Human).
Water	96·536	90·237	90·48
Solids	3·454	9·763	9·52
Solids—			
Proteids, including Serum-Albumin, Fibrin, and Globulin.	1·320	3·886	7·08
Extractives, including in (1 and 1) Sugar, Urea, Leucin & Cholesterin	1·559	1·565	·108
Fatty matter	a trace	3·601	·92
Salts	·585	·711	·44

From the above analyses of lymph and chyle, it appears that they contain essentially the same constituents that are found in the blood. Their composition, indeed, differs from that of the blood in degree rather than in kind. They do not, however, unless by accident, contain coloured corpuscles.

Quantity.—The quantity which would pass into a cat's blood in twenty-four hours has been estimated to be equal to about one-sixth of the weight of the whole body. And, since the estimated weight of the blood in cats is to the weight of their bodies as 1·7, the quantity of lymph daily traversing the thoracic duct would appear to be about equal to the quantity of blood at any time contained in the animals. By another series of experiments, the quantity of lymph traversing the thoracic duct of a dog in twenty-four hours was found to be about equal to two-thirds of the blood in the body. (Bidder and Schmidt.)

Absorption by the Lacteals.—During the passage of the chyme along the whole tract of the intestinal canal, its completely digested parts are absorbed by the blood-vessels and lacteals distributed in the mucous membrane. The blood-vessels appear to absorb chiefly the dissolved portions of the food, and these, including especially the albuminous and saccharine, they imbibe without choice; whatever can mix with the blood passes into the vessels, as will be presently described. But the lacteals appear to absorb only certain constituents of the food, including particularly the fatty portions. The absorption by both sets of vessels is carried on most actively but not exclusively, in the villi of the small intestine; for in these minute processes, both the capillary blood-vessels and the lacteals are brought almost into contact with the intestinal contents. There seems to be no doubt that absorption of fatty matters during digestion, from the contents of the intestines, is effected chiefly between the epithelial cells which line the intestinal tract (Watney), and especially those which clothe the surface of the villi. Thence, the fatty particles are passed on into the interior of the lacteal vessels (fig. 216, *a*), but how they pass, and what laws govern their so doing, are not at present exactly known.

The process of absorption is assisted by the pressure exercised on the contents of the intestines by their contractile walls; and the absorption of fatty particles is also facilitated by the presence of the bile, and the pancreatic and intestinal secretions, which moisten the absorbing surface. For it has been found by experiment, that the passage of oil through an animal membrane is made much easier when the latter is impregnated with an alkaline fluid.

Absorption by the Lymphatics.—The real source of the lymph, and the mode in which its absorption is effected by the lymphatic vessels, were long matters of discussion. But the problem has been much simplified by more accurate knowledge of the anatomical relations of the lymphatic capillaries. The lymph is, without doubt, identical in great part, with the *liquor sanguinis*, which, as before remarked, is always exuding from the blood-capillaries into the interstices of the tissues in which they lie; and as these interstices form in most parts of the body the beginnings of the lymphatics, the source of the lymph is sufficiently obvious. In connection with this may be mentioned the fact that changes in the character of the lymph correspond very closely with changes in the character of either the whole mass of blood, or of that in the vessels of the part from which the lymph is exuded. Thus it appears that the coagulability of the lymph is directly proportionate to that of the blood; and that when fluids are injected into the blood-vessels in sufficient quantity to distend them, the injected substance may be almost directly afterwards found in the lymphatics.

Some other matters than those originally contained in the exuded liquor sanguinis may, however, find their way with it into the lymphatic vessels. Parts which having entered into the composition of a tissue, and, having fulfilled their purpose, require to be removed, may not be altogether excrementitious, but may admit of being re-organised and adapted again for nutrition; and these may be absorbed by the lymphatics, and elaborated with the other contents of the lymph in passing through the glands.

Lymph-Hearts.—In reptiles and some birds, an important auxiliary to the movement of the lymph and chyle is supplied in certain muscular sacs, named *lymph-hearts* (fig. 217), and it has been shown that the caudal heart of the eel is a lymph-heart also. The number and position of these organs vary. In frogs and toads there are usually four, two anterior and two posterior; in the frog, the posterior lymph-heart on each side is situated in the ischiatic region, just beneath the skin; the anterior lies deeper, just over the transverse process of the third vertebra. Into each of these cavities several lymphatics open, the orifices of the vessels being guarded by valves, which prevent the retrograde passage of the lymph. From each heart a single vein proceeds and conveys the lymph directly into the venous system. In the frog, the inferior lymphatic heart, on each side, pours its lymph into a branch of the ischiatic vein; by the superior, the lymph is forced into a branch of the jugular vein, which issues from its anterior surface, and which becomes turgid each time that the sac contracts. Blood is prevented from passing from the vein into the lymphatic heart by a valve at its orifice.

The muscular coat of these hearts is of variable thickness; in some cases it can only be discovered by means of the microscope; but in every case it is composed of striped fibres. The contractions of the hearts are rhythmical, occurring about sixty times in a minute, slowly, and, in comparison with those of the blood-hearts, feebly. The pulsations of the cervical pair are not always synchronous with those of the pair in the ischiatic region, and even the corresponding sacs of opposite sides are not always synchronous in their action.

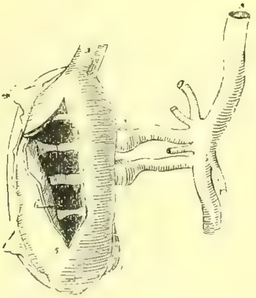

Fig. 217.—*Lymphatic heart* (9 *lines long*, 4 *lines broad*) *of a large species of serpent, the Python bivittatus.* 4. The external cellular coat. 5. The thick muscular coat. Four muscular columns run across its cavity, which communicates with three lymphatics (1—only one is seen here), and with two veins (2, 2). 6. The smooth lining membrane of the cavity. 7. A small appendage, or auricle, the cavity of which is continuous with that of the rest of the organ (after E. Weber).

Unlike the contractions of the blood-heart, those of the lymph-heart appear to be directly dependent upon a certain limited portion of the spinal cord. For Volkmann found that so long as the portion of spinal cord corresponding to the third vertebra of the frog was uninjured, the cervical pair of lymphatic hearts continued pulsating after all the rest of the spinal cord and the brain were destroyed; while destruction of this portion, even though all other parts of the nervous centres were uninjured, instantly arrested the heart's movements. The posterior, or ischiatic, pair of lymph-hearts were found to be governed, in like manner, by the portion of spinal cord corresponding to the eighth vertebra. Division of the posterior spinal roots did not arrest the movements; but division of the anterior roots caused them to cease at once.

Absorption by Blood-vessels.—In the absorption by the lymphatic or lacteal vessels just described, there appears something like the exercise of choice in the materials admitted into them. But the absorption by blood-vessels presents no such appearance of selection of materials; rather, it appears, that every substance, whether gaseous, liquid, or a soluble, or minutely divided solid, may be absorbed by the blood-vessels, provided it is capable of permeating their walls, and of mixing with the blood; and that of all such substances, the mode and measure of absorption are determined solely by their physical or chemical properties and conditions, and by those of the blood and the walls of the blood-vessels.

Osmosis.—The phenomena are, indeed, to a great extent, comparable to that passage of fluids through membrane, which occurs quite independently of vital conditions, and the earliest and best scientific investigation of which was made by Dutrochet. The instrument which he employed in his experiments was named an *endosmometer*. It may consist of a graduated tube expanded into an open-mouthed bell at one end, over which a portion of membrane is tied (fig. 218). If now the bell be filled with a solution of a salt—say sodium chloride, and be immersed in water, the water will pass into the solution, and part of the salt will pass out into the water; the water, however, will pass into the solution much more rapidly than the salt will pass out into the water, and the diluted solution will rise in the tube. To this passage of fluids through membrane the term *Osmosis* is applied.

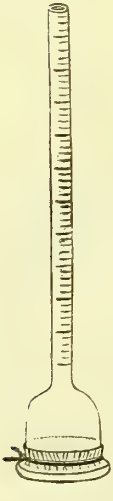

Fig. 218.—Endosmometer.

The nature of the membrane used as a septum, and its affinity for the fluids subjected to experiment have an important influence, as might be anticipated, on the rapidity and duration of the osmotic current. Thus, if a piece of ordinary bladder be used as the septum between water and alcohol, the current is almost solely from the water to the alcohol, on account of the much greater affinity of water for this kind of membrane; while, on the other hand, in the case of a membrane of caoutchouc, the alcohol, from its greater affinity for this substance, would pass freely into the water.

Osmosis by Blood-vessels.—Absorption by blood-vessels is the consequence of their walls being, like the membranous septum of the endosmometer, porous and capable of imbibing fluids, and of the blood being so composed that most fluids will mingle with it. The process of absorption, in an instructive, though very imperfect degree, may be observed in any portion of vascular tissue removed from the body. If such a one be placed in a vessel of water, it will shortly swell, and become heavier and moister, through the quantity of water imbibed or soaked into it; and if now, the blood contained in any of its vessels be let out, it will be found diluted with water, which has been absorbed by the blood-vessels and mingled with the blood. The water round the piece of tissue also will become blood-stained; and if all be kept at perfect rest, the stain derived from the solution of the colouring matter of the blood (together with which chemistry would detect some of the albumen and other parts of the liquor sanguinis) will spread more widely every day. The same will happen if the piece of tissue be placed in a saline solution instead of water, or in a solution of colouring or odorous matter, either of which will give their tinge or smell to the blood, and receive, in exchange, the colour of the blood.

Colloids and Crystalloids.—Various substances have been classified according to the degree in which they possess the property of passing, when in a state of solution in water, through membrane; those which pass freely, inasmuch as they are usually capable of crystallization, being termed *crystalloids*, and those which pass with difficulty, on account of their, physically, glue-like characters, *colloids*. (Graham.)

This distinction, however, between colloids and crystalloids which is made the basis of their classification, is by no means the only difference between them. The colloids, besides the absence of power to assume a crystalline form, are characterised by their inertness as acids or bases, and feebleness in all ordinary chemical relations. Examples of them are found in albumin, gelatin, starch, hydrated alumina, hydrated silicic acid, etc.; while the crystalloids are characterised by qualities the reverse of those just mentioned as belonging to colloids. Alcohol, sugar, and ordinary saline substances are examples of crystalloids.

Rapidity of Absorption.—The rapidity with which matters may be absorbed from the stomach, probably by the blood-vessels chiefly, and diffused through the textures of the body, may be gathered from the history of some experiments. From these it appears that even in a quarter of an hour after being given on an empty stomach, lithium chloride may be diffused into all the vascular textures of the body, and into some of the non-vascular, as the cartilage of the hip-joint, as well as into the aqueous humour of the eye. Into the outer part of the crystalline lens it may pass after a time, varying from half an hour to an hour and a half. Lithium carbonate, when taken in five or ten-grain doses on an empty stomach, may be detected in the urine in 5 or 10 minutes; or, if the stomach be full at the time of taking the dose, in 20 minutes. It may sometimes be detected in the urine, moreover, for six, seven, or eight days. (Bence Jones.)

Some experiments on the absorption of various mineral and vegetable poisons, have brought to light the singular fact, that, in some cases, absorption takes place more rapidly from the rectum than from the stomach. Strychnia, for example, when in solution, produces its poisonous effects much more speedily when introduced into the rectum than into the stomach. When introduced in the solid form, however, it is absorbed more rapidly from the stomach than from the rectum, doubtless because of the greater solvent property of the secretion of the former than of that of the latter. (Savory.)

With regard to the degree of absorption by living blood-vessels, much depends on the facility with which the substance to be absorbed can penetrate the membrane or tissue which lies between it and the blood-vessels. Thus, absorption will hardly take place through the epidermis, but is quick when the epidermis is removed, and the same vessels are covered with only the surface of the cutis, or with granulations. In general, the absorption through membranes is in an inverse proportion to the thickness of their epithelia; so that the urinary bladder of a frog is traversed in less than a second; and the absorption of poisons by the stomach or lungs appears sometimes accomplished in an immeasurably small time.

Conditions for Absorption.—1. The substance to be absorbed must, as a general rule, be in the liquid or gaseous state, or, if a solid, must be soluble in the fluids with which it is brought in contact. Hence the marks of tattooing, and the discoloration produced by silver nitrate taken internally, remain. Mercury may be absorbed even in the metallic state; and in that state may pass into and remain in the blood-vessels, or be deposited from them; and such substances as exceedingly finely-divided charcoal, when taken into the alimentary canal, have been found in the mesenteric veins; the insoluble materials of ointments may also be rubbed into the blood-vessels; but there are no facts to determine how these various substances effect their passage. Oil, minutely divided, as in an emulsion, will pass slowly into blood-vessels, as it will through a filter moistened with water; and, without doubt, fatty matters find their way into the blood-vessels as well as the lymph-vessels of the intestinal canal, although the latter seem to be specially intended for their absorption.

2. The less dense the fluid to be absorbed, the more speedy, as a general rule, is its absorption by the living blood-vessels. Hence the rapid absorption of water from the stomach; also of weak saline solutions; but with strong solutions, there appears less absorption into, than effusion from, the blood-vessels.

3. The absorption is the less rapid the fuller and tenser the blood-vessels are; and the tension may be so great as to hinder altogether the entrance of more fluid. Thus, if water is injected into a dog's veins to repletion, poison is absorbed very slowly; but when the tension of the vessels is diminished by bleeding, the poison acts quickly. So, when cupping-glasses are placed over a poisoned wound, they retard the absorption of the poison not only by diminishing the velocity of the circulation in the part, but by filling all its vessels too full to admit more.

On the same ground, absorption is the quicker the more rapid the circulation of the blood; not because the fluid to be absorbed is more quickly imbibed into the tissues, or mingled with the blood, but because as fast as it enters the blood, it is carried away from the part, and the blood being constantly renewed, is constantly as fit as at the first for the reception of the substance to be absorbed.

CHAPTER X.

ANIMAL HEAT.

The Average Temperature of the human body in those *internal* parts which are most easily accessible, as the mouth and rectum, is from 98·5° to 99·5° F. (36·9°—37·4° C.). In different parts of the *external* surface of the human body the temperature varies only to the extent of two or three degrees (F.), when all are alike protected from cooling influences; and the difference which under these circumstances exists, depends chiefly upon the different degrees of blood-supply. In the arm-pit—the most convenient situation, under ordinary circumstances, for examination by the thermometer—the average temperature is 98·6° F. (36·9° C.). In different internal parts, the variation is one or two degrees; those parts and organs being warmest which contain most blood, and in which there occurs the greatest amount of chemical change, *e.g.*, the glands and the muscles; and the temperature is highest, of course, when they are most actively working: while those tissues which, subserving only a mechanical function, are the seat of least active circulation and chemical change, are the coolest. These differences of temperature, however, are actually but slight, on account of the provisions which exist for maintaining uniformity of temperature in different parts.

Circumstances causing Variations in Temperature.—The chief circumstances by which the temperature of the healthy body is influenced are the following:—*Age; Sex; Period of the day; Exercise; Climate and Season; Food and Drink.*

Age.—The average temperature of the new-born child is only about 1° F. (·54° C.) above that proper to the adult; and the difference becomes still more trifling during infancy and early childhood. The temperature falls to the extent of about ·2°—·5° F. from early infancy to puberty, and by about the same amount from puberty to fifty or sixty years of age. In old age the temperature again rises, and approaches that of infancy; but although this is the case, yet the power of resisting cold is less in them—

exposure to a low temperature causing a greater reduction of heat than in young persons.

The same rapid diminution of temperature has been observed to occur in the new-born young of most carnivorous and rodent animals when they are removed from the parent, the temperature of the atmosphere being between 50° and 53·5° F. (10°-12° C.); whereas while lying close to the body of the mother, their temperature is only 2 or 3 degrees F. lower than hers. The same law applies to the young of birds.

Sex.—The average temperature of the female would appear to be very slightly higher than that of the male.

Period of the Day. — The temperature undergoes a gradual alteration, to the extent of about 1° to 1·5° F. (·54—·8° C.) in the course of the day and night; the *minimum* being at night or in the early morning, the *maximum* late in the afternoon.

Exercise.—Active exercise raises the temperature of the body from 1° to 2° F. (·54°—1·08° C.). This may be partly ascribed to generally increased combustion-processes, and partly to the fact, that every muscular contraction is attended by the development of one or two degrees of heat in the acting muscle; and that the heat is increased according to the number and rapidity of these contractions, and is quickly diffused by the blood circulating from the heated muscles. Possibly, also, some heat may be generated in the various movements, stretchings, and recoilings of the other tissues, as the arteries, whose elastic walls, alternately dilated and contracted, may give out some heat, just as caoutchouc alternately stretched and recoiling becomes hot. But the heat thus developed cannot be great. The great apparent increase of heat during exercise depends, in a great measure, on the increased circulation and quantity of blood, and, therefore, greater heat, in parts of the body (as the skin, and especially the skin of the extremities), which, at the same time that they feel more acutely than others any changes of temperature, are, under ordinary conditions, by some degrees colder than organs more centrally situated.

Climate and Season.—The temperature of the human body is the same in temperate and tropical climates. (Johnson, Boileau, Furnell.) In summer the temperature of the body is a little higher than in winter; the difference amounting to about a third of a degree F. (Wunderlich.)

Food and Drink.—The effect of a meal upon the temperature of a body is but small. A very slight rise usually occurs. Cold alcoholic drinks depress the temperature somewhat (·5° to 1° F.). Warm alcoholic drinks, as well as warm tea and coffee, raise the temperature (about ·5° F.).

In disease the temperature of the body deviates from the normal standard to a greater extent than would be anticipated from the slight effect of external conditions during health. Thus, in some diseases, as pneumonia and typhus, it occasionally rises as high as 106° or 107° F. (41°—41·6° C.); and considerably higher temperatures have been noted. In Asiatic cholera, on the other hand, a thermometer placed in the mouth may sometimes rise only to 77° or 79° F. (25°—26·2° C.).

The temperature maintained by Mammalia in an active state of life, according to the tables of Tiedemann and Rudolphi, averages 101° (38.3° C.) The extremes recorded by them were 96° and 106°, the former in the narwhal, the latter in a bat (Vespertilio pipistrella). In Birds, the average is as high as 107° (41·2° C.; the highest temperature, 111·25° (46·2° C.); being in the small species, the linnets, &c. Among Reptiles, while the medium they were in was 75° (23·9° C.) their average temperature, was 82·5° (31·2° C.). As a general rule, their temperature, though it falls with that of the surrounding medium, is, in temperate media, two or more degrees higher; and though it rises also with that of the medium, yet at very high degrees it ceases to do so, and remains even lower than that of the medium. Fish and invertebrata present, as a general rule, the same temperature as the medium in which they live, whether that be high or low; only among fish, the tunny tribe, with strong hearts and red meat-like muscles, and more blood than the average of fish have, are generally 7° (3·8° C.) warmer than the water around them.

The difference, therefore, between what are commonly called the warm and the cold-blooded animals, is not one of absolutely higher or lower temperature: for the animals which to us in a temperate climate, feel cold (being like the air or water, colder than the surface of our bodies), would in an external temperature of 100° (37·8° C.) have nearly the same temperature and feel hot to us. The real difference is that what we call warm-blooded animals (Birds and Mammalia), have a certain "permanent heat in all atmospheres," while the temperature of the others, which we call cold-blooded, is "variable with every atmosphere." (Hunter.)

The power of maintaining a uniform temperature, which Mammalia and Birds possess, is combined with the want of power to endure such changes of body temperature as are harmless to the other classes; and when their power of resisting change of temperature ceases, they suffer serious disturbance or die.

Sources and Mode of Production of Heat in the Body.—The heat which is produced in the body arises from combustion, and is due to the fact that the oxygen of the atmosphere taken into the system is combined with the carbon and hydrogen of the tissues. Any changes which occur in the protoplasm of the tissues, resulting in an exhibition of their function, is attended by the evolution of heat and also by the production of carbonic acid and water; and the more active the changes, the greater the heat produced and the greater the amount of the carbonic acid and water formed. But in order that the protoplasm may perform its function, the waste of its own tissue (destructive metabolism), must be repaired by the supply of food material, and therefore for the production of heat it is necessary to supply food. In the tissues, therefore, two processes are continually going on: the building up of the protoplasm from the food (constructive metabolism), which is not accompanied by the evolution of heat but possibly by the reverse, and the oxidation of the protoplastic materials, resulting in the production of energy, by which heat is produced and carbonic acid and water are evolved. Some heat will also be generated in the combination of sulphur and phosphorus with oxygen, but the amount thus produced is but small.

It is not necessary to assume that the combustion processes, which ultimately issue in the production of carbonic acid and water, are as simple as the bare statement of the fact might seem to indicate. But complicated as the various stages of combustion may be, the ultimate result is as simple as in ordinary combustion outside the body, and the products are the same. The same amount of heat will be evolved in the union of any given quantities of carbon and oxygen, and of hydrogen and oxygen, whether the combination be rapid and direct, as in ordinary combustion, or slow and almost imperceptible, as in the changes which occur in the living body. And since the heat thus arising will be distributed wherever the blood is carried, every part of the body will be heated equally, or nearly so.

This theory, that the maintenance of the temperature of the living body depends on continual chemical change, chiefly by oxidation, of combustible materials existing in the tissues, has long been established by the demonstration that the quantity of carbon and hydrogen which, in a given time, unites in the body with oxygen, is sufficient to account for the amount of heat generated in the animal within the same time: an amount capable of maintaining the temperature of the body at from 98°—100° F.

(36·8°—37·8° C.), notwithstanding a large loss by radiation and evaporation.

It should be remembered that heat may be introduced into the body by means of warm drinks and foods, and, again, that it is possible for the preliminary digestive changes to be accompanied by the evolution of heat.

Chief Heat-producing Tissues. — The chemical changes which produce the body-heat appear to be especially active in certain tissues :—(1), In the *Muscles*, which form so large a part of the organism. The fact that the manifestation of muscular energy is always attended by the evolution of heat and the production of carbonic acid has been demonstrated by actual experiment ; and when not actually in a condition of active contraction, a metabolism, not so active but still actual, goes on, which is accompanied by the manifestation of heat. The total amount set free by the muscles, therefore, must be very great ; and it has been calculated that even neglecting the heat produced by the quiet metabolism of muscular tissue, the amount of heat generated by muscular activity supplies the principal part of the total heat produced within the body. (2), In the *Secreting glands*, and principally in the liver as being the largest and most active. It has been found by experiment that the blood leaving the glands is considerably warmer than that entering them. The metabolism in the glands is very active and, as we have seen, the more active the metabolism the greater the heat produced. (3), In *the Brain ;* the venous blood having a higher temperature than the arterial. It must be remembered, however, that although the organs above mentioned are the chief heat-producing parts of the body, all living tissues contribute their quota, and this in direct proportion to their activity. The blood itself is also the seat of metabolism, and, therefore, of the production of heat ; but the share which it takes in this respect, apart from the tissues in which it circulates, is very inconsiderable.

Regulation of the Temperature of the Human Body.— The average temperature of the body is maintained under different conditions of external circumstances by mechanisms which permit of (1) variation in the amount of heat got rid of, and (2) variations in the amount of heat produced or introduced into the body. In healthy warm-blooded animals the loss and gain of heat are so nearly balanced one by the other that, under all ordinary circumstances, an uniform temperature, within two or three degrees, is preserved.

I. Methods of Variation in the amount of Heat got rid of.—The loss of heat from the human body is principally regulated by the amount lost by radiation and conduction from its surface, and by means of the constant evaporation of water from the same part, and (2) to a much less degree from the air-passages; in each act of respiration, heat is lost to a greater or less extent according to the temperature of the atmosphere; unless indeed the temperature of the surrounding air exceed that of the blood. We must remember too that all food and drink which enter the body at a lower temperature than itself abstract a small measure of heat: while the urine and fæces which leave the body at about its own temperature are also means by which a small amount is lost.

(*a.*) *Loss of Heat from the Surface of the Body: the Skin.*—By far the most important loss of heat from the body,—probably 70 or 80 per cent. of the whole amount, is that which takes place by radiation, conduction, and evaporation from the skin. The means by which the skin is able to act as one of the most important organs for regulating the temperature of the blood, are—(1), that it offers a large surface for radiation, conduction, and evaporation; (2), that it contains a large amount of blood; (3), that the quantity of blood contained in it is the greater under those circumstances which demand a loss of heat from the body, and *vice versâ* For the circumstance which directly determines the quantity of blood in the skin, is that which governs the supply of blood to all the tissues and organs of the body, namely, the power of the vaso-motor nerves to cause a greater or less tension of the muscular element in the walls of the arteries, and, in correspondence with this, a lessening or increase of the calibre of the vessel, accompanied by a less or greater current of blood. A warm or hot atmosphere so acts on the nerve fibres of the skin, as to lead them to cause in turn a relaxation of the muscular fibre of the blood-vessels; and, as a result, the skin becomes full-blooded, hot, and sweating; and much heat is lost. With a low temperature, on the other hand, the blood-vessels shrink, and in accordance with the consequently diminished blood-supply, the skin becomes pale, and cold, and dry; and no doubt a similar effect may be produced through the vasomotor centre in the medulla and spinal cord. Thus, by means of a self-regulating apparatus, the skin becomes the most important of the means by which the temperature of the body is regulated.

In connection with loss of heat by the skin, reference has been made to that which occurs both by radiation and conduction, and by evaporation; and the subject of animal heat has been considered almost solely with regard to the ordinary case of man living in a medium colder than his body, and therefore losing heat in all the ways mentioned. The importance of the means however, adopted, so to speak, by the skin for regulating the temperature of the body, will depend on the conditions by which it is surrounded; an inverse proportion existing in most cases between the loss by radiation and conduction on the one hand, and by evaporation on the other. Indeed, the small loss of heat by evaporation in cold climates may go far to compensate for the greater loss by radiation; as, on the other hand, the great amount of fluid evaporated in hot air may remove nearly as much heat as is commonly lost by both radiation and evaporation in ordinary temperatures; and thus, it is possible that the quantities of heat required for the maintenance of an uniform proper temperature in various climates and seasons are not so different as they, at first thought, seem.

Many examples may be given of *the power which the body possesses of resisting the effects of a high temperature*, in virtue of evaporation from the skin. Blagden and others supported a temperature varying between 198°—211° F. (92°—100° C.) in dry air for several minutes; and in a subsequent experiment he remained eight minutes in a temperature of 260 F. (126·5° C.). "The workmen of Sir F. Chantrey were accustomed to enter a furnace, in which his moulds were dried, whilst the floor was red-hot, and a thermometer in the air stood at 350° F. (177·8° C.) and Chabert, the fire-king, was in the habit of entering an oven the temperature of which was from 400° to 600°," F. (205°—315° C.) (Carpenter.)

But such heats are not tolerable when the air is moist as well as hot, so as to prevent evaporation from the body. C. James states, that in the vapour baths of Nero he was almost suffocated in a temperature of 112° F. (44·5° C.), while in the caves of Testaccio, in which the air is dry, he was but little incommoded by a temperature of 176° F. (80° C.). In the former, evaporation from the skin was impossible; in the latter it was abundant, and the layer of vapour which would rise from all the surface of the body would, by its very slowly conducting power, defend it for a time from the full action of the external heat.

(The glandular apparatus, by which secretion of fluid from the skin is effected, will be considered in the Section on the Skin.)

The ways by which the skin may be rendered more efficient as a cooling-apparatus by exposure, by baths, and by other means which man instinctively adopts for lowering his temperature when necessary, are too well known to need more than to be mentioned.

Although under any ordinary circumstances, the external application of cold only temporarily depresses the temperature to a slight extent, it is otherwise in cases of high temperature in fever. In these cases a tepid bath may reduce the temperature several degrees, and the effect so produced lasts in some cases for many hours.

(*b.*) *Loss of Heat from the Lungs.*—As a means for lowering the temperature, the lungs and air-passages are very inferior to the skin; although, by giving heat to the air we breathe, they stand next to the skin in importance. As a *regulating* power, the inferiority is still more marked. The air which is expelled from the lungs leaves the body at about the temperature of the blood, and is always saturated with moisture. No inverse proportion, therefore, exists between the loss of heat by radiation and conduction on the one hand, and by evaporation on the other. The colder the air, for example, the greater will be the loss in all ways. Neither is the quantity of blood which is exposed to the cooling influence of the air diminished or increased, so far as is known, in accordance with any need in relation to temperature. It is true that by varying the number and depth of the respirations, the quantity of heat given off by the lungs may be made, to some extent, to vary also. But the respiratory passages, while they must be considered important means by which heat is lost, are altogether subordinate, in the power of regulating the temperature, to the skin.

(*c.*) *By Clothing.*—The influence of external coverings for the body must not be unnoticed. In warm-blooded animals, they are always adapted, among other purposes, to the maintenance of uniform temperature ; and man adapts for himself such as are, for the same purpose, fitted to the various climates to which he is exposed. By their means, and by his command over food and fire, he maintains his temperature on all accessible parts of the surface of the earth.

II. Methods of Variation in the Amount of Heat Produced.—It may seem to have been assumed, in the foregoing pages, that the only regulating apparatus for temperature required by the human body is one that shall, more or less, produce a *cooling* effect ; and as if the amount of heat produced were always, therefore, in excess of that which is required. Such an assumption would be incorrect. We have the power of regulating the production of heat, as well as its loss.

(*a*) *By Regulating the Quantity and Quality of the Food taken.*—In food we have a means for elevating our temperature. It is the fuel, indeed, on which animal heat ultimately depends altogether. Thus, when more heat is wanted, we instinctively take more food, and take such kinds of it as are good for combustion ; while every-day experience shows the different power of resisting cold possessed, respectively, by the well-fed and by the starved. In northern regions, again, and in the colder seasons of more southern climes, the quantity of food consumed is (speaking very generally) greater than that consumed by the same men or animals in opposite conditions of climate and season. And the food which appears naturally adapted to the inhabitants of the coldest climates, such as the several fatty and oily substances, abounds in carbon and hydrogen, and is fitted to combine with the large quantities of oxygen which, breathing cold dense air, they absorb from their lungs.

(*b.*) *By Exercise.*—In exercise, we have an important means of raising the temperature of our bodies (p. 383).

(*c.*) *By Influence of the Nervous System.*—The influence of the nervous system in modifying the production of heat must be very important, as upon nervous influence depends the amount of the metabolism of the tissues. The experiments and observations which best illustrate it are those showing, first, that when the supply of nervous influence to a part is cut off, the temperature of that part falls below its ordinary degree ; and, secondly, that when death is caused by severe injury to, or removal of, the nervous centres, the temperature of the body rapidly falls, even though artificial respiration be performed, the circulation maintained, and to all appearance the ordinary chemical changes of the body be completely effected. It has been repeatedly noticed, that after division of the nerves of a limb its temperature falls; and this diminution of heat has been remarked still more plainly in limbs deprived of nervous influence by paralysis.

With equal certainty, though less definitely, the influence of the nervous system on the production of heat, is shown in the rapid and momentary increase of temperature, sometimes general, at other times quite local, which is observed in states of nervous excitement; in the general increase of warmth of the body, sometimes amounting to perspiration, which is excited by passions of the mind; in the sudden rush of heat to the face, which is not a mere sensation; and in the equally rapid diminution of temperature in the depressing passions. But none of these instances suffice to prove that heat is generated by mere nervous action, independent of any chemical change; all are explicable, on the supposition that the nervous system alters, by its power of controlling the calibre of the blood-vessels, the quantity of blood supplied to a part; while any influence which the nervous system may have in the production of heat, apart from this influence on the blood-vessels, is an indirect one, and is derived from its power of causing such nutritive change in the tissues as may, by involving the necessity of chemical action, involve the production of heat.

Inhibitory heat-centre.—Whether a centre exists which regulates the production of heat in warm-blooded animals, is still undecided. Experiments have shown that exposure to cold at once increases the oxygen taken in, and the carbonic acid given out, indicating an increase in the activity of the metabolism of the tissues, but that in animals poisoned by urari, exposure to cold diminishes both the metabolism and the temperature, and warm-blooded animals then re-act to variations of the external temperature just in the same way as cold-blooded. These experiments seem to suggest that there is a centre, to which, under normal circumstances, the impression of cold is conveyed, and from which by efferent nerves impulses pass to the muscles, whereby an increased metabolism is induced, and so an increased amount of heat is generated. The centre is probably situated above the medulla. Thus in urarised animals, as the nerves to the muscles, the metabolism of which is so important in the production of heat, are paralyzed, efferent impulses from the centre cannot induce the necessary metabolism for the production of heat, even though afferent impulses from the skin, stimulated by the alteration of temperature, have conveyed to it the necessity of altering the amount of heat to be produced. The same effect is produced when the medulla is cut.

Influence of Extreme Heat and Cold.—In connection with the regulation of animal temperature, and its maintenance in health at the normal height, may be noted the result of circumstances too powerful, either in raising or lowering the heat of the body, to be controlled by the proper regulating apparatus. Walther found that rabbits and dogs, when tied to a board and exposed to a hot sun, reached a temperature of 114·8° F., and then died. Cases of sunstroke furnish us with several examples in the case of man; for it would seem that here death ensues chiefly or solely from elevation of the temperature. In many febrile diseases the immediate cause of death appears to be the elevation of the temperature to a point inconsistent with the continuance of life.

The effect of mere loss of bodily temperature in man is less well known than the effect of heat. From experiments by Walther, it appears that rabbits can be cooled down to 48° F. (8·9° C.), before they die, if artificial respiration be kept up. Cooled down to 64° F. (17·8° C.), they cannot recover unless external warmth be applied together with the employment of artificial respiration. Rabbits not cooled below 77° F. (25° C.) recover by external warmth alone.

CHAPTER XI.

SECRETION.

Secretion is the process by which materials are separated from the blood, and from the organs in which they are formed, for the purpose either of serving some ulterior office in the economy, or of being discharged from the body as useless or injurious. In the former case, the separated materials are termed *secretions;* in the latter, they are termed *excretions.*

Most of the secretions consist of substances which, probably, do not pre-exist in the same form in the blood, but require special organs and a process of elaboration for their formation, *e.g.*, the liver for the formation of bile, the mammary gland for the formation of milk. The excretions, on the other hand, commonly or chiefly consist of substances which exist ready-formed in the blood, and are merely abstracted therefrom. If from any cause, such as extensive disease or extirpation of an excretory organ, the separation of an excretion is prevented, and an accumulation of it in the blood ensues, it frequently escapes through other organs, and may be detected in various fluids of the body. But this is never the case with secretions; at least with those that are most elaborated; for after the removal of the special organs by which any of them is elaborated, it is no longer formed. Cases sometimes occur in which the secretion continues to be formed by the natural organ, but not being able to escape towards the exterior, on account of some obstruction, is re-absorbed into the blood, and afterwards discharged from it by exudation in other ways; but these are not instances of true vicarious secretion, and must not be thus regarded.

These circumstances, and their final destination, are, however, the only particulars in which secretions and excretions can be distinguished; for, in general, the structure of the parts engaged in eliminating excretions is as complex as that of the parts concerned in the formation of secretions. And since the differences of the two processes of separation, corresponding with those in the several purposes and destinations of the fluids, are not yet ascertained, it will be sufficient to speak in general terms of the process of separation or secretion.

Every secreting apparatus possesses, as essential parts of its structure, a simple and almost textureless membrane, named the *primary* or *basement-membrane ;* certain *cells ;* and *blood-vessels.* These three structural elements are arranged together in various ways ; but all the varieties may be classed under one or other of two principal divisions, namely, *membranes* and *glands.*

Organs and Tissues of Secretion.

The principal secreting membranes are (1) the Serous and Synovial membranes ; (2) the Mucous membranes ; (3) the Mammary gland ; (4) the Lachrymal gland ; and (5) the Skin.

(1) **Serous Membranes.**—The serous membranes are especially distinguished by the characters of the endothelium covering their free surface : it always consists of a single layer of polygonal cells. The ground substance of most serous membranes consists of connective - tissue corpuscles of various forms lying in the branching spaces which constitute the "lymph canalicular system" (p. 363), and interwoven with bundles of white fibrous tissue, and numerous delicate elastic fibrillæ, together with blood - vessels, nerves, and lymphatics. In relation to the process of secretion, the layer of connective tissue serves as a ground-work for the ramification of blood-vessels, lymphatics, and nerves. But in its usual form it is absent in some instances, as in the arachnoid covering the dura mater,

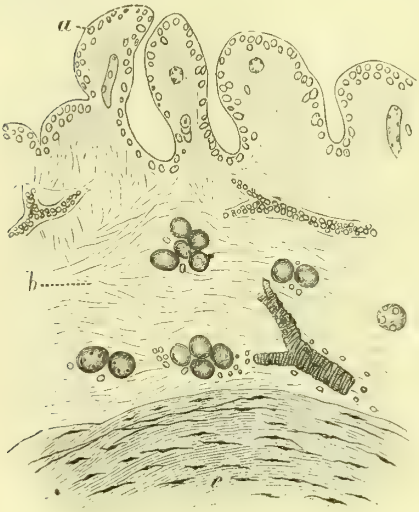

Fig. 219.—*Section of synovial membrane.* *a*, endothelial covering of elevations of the membrane ; *b*, subserous tissue containing fat and blood-vessels ; *c*, ligament covered by the synovial membrane. (Cadiat.)

and in the interior of the ventricles of the brain. The primary membrane and epithelium are always present, and are concerned in the formation of the fluid by which the free surface of the membrane is moistened.

Serous membranes are of two principal kinds; 1*st.* Those which line visceral cavities,—the *arachnoid*, *pericardium*, *pleuræ*, *peritoneum*, and *tunicæ vaginales.* 2*nd.* The *synovial membranes* lining the joints, and the sheaths of tendons and ligaments, with which, also, are usually included the *synovial bursæ*, or *bursæ mucosæ*, whether these be subcutaneous, or situated beneath tendons that glide over bones.

The serous membranes form closed sacs, and exist wherever the free surfaces of viscera come into contact with each other or lie in cavities unattached to surrounding parts. The viscera invested by a serous membrane are, as it were, pressed into the shut sac which it forms, carrying before them a portion of the membrane, which serves as their investment. To the law that serous membranes form shut sacs, there is, in the human subject, one exception, viz.: the opening of the Fallopian tubes into the abdominal cavity,—an arrangement which exists in man and all Vertebrata, with the exception of a few fishes.

Functions.—The principal purpose of the serous and synovial membranes is to furnish a smooth, moist surface, to facilitate the movements of the invested organ, and to prevent the injurious effects of friction. This purpose is especially manifested in joints, in which free and extensive movements take place; and in the stomach and intestines, which, from the varying quantity and movements of their contents, are in almost constant motion upon one another and the walls of the abdomen.

Serous Fluid.—The fluid secreted from the free surface of the serous membranes is, in health, rarely more than sufficient to ensure the maintenance of their moisture. The opposed surfaces of each serous sac are at every point in contact with each other. After death, a larger quantity of fluid is usually found in each serous sac; but this, if not the product of manifest disease, is probably such as has transuded after death, or in the last hours of life. An excess of such fluid in any of the serous sacs constitutes dropsy of the sac.

The fluid naturally secreted by the serous membranes appears to be identical, in general and chemical characters, with the serum of the blood, or with very dilute liquor sanguinis. It is of a pale yellow or straw-colour, slightly viscid, alkaline, and, on account of the presence of albumen, coagulable by heat. This similarity of the serous fluid to the liquid part of blood, and to the fluid with which most animal tissues are moistened, renders it probable that it is, in great measure, separated by simple transudation, through the walls of the blood-vessels. The probability is increased by the fact that, in jaundice, the fluid in the serous sacs is, equally with the serum of the blood, coloured with the bile. But there is reason for supposing that the fluid of the cerebral ventricles and of the arachnoid sac are exceptions to this rule; for they differ from the fluids of the other serous sacs not only in being pellucid, colourless, and of much less specific gravity, but in that they seldom receive the tinge of bile when present in the blood, and are not coloured by madder, or other similar substances introduced abundantly into the blood.

Synovial Fluid: Synovia.—It is also probable that the formation of synovial fluid is a process of more genuine and elaborate secretion, by means of the epithelial cells on the surface of the membrane, and especially of those which are accumulated on the edges and processes of the synovial fringes; for, in its peculiar density, viscidity, and abundance of albumin, synovia differs alike from the serum of blood and from the fluid of any of the serous cavities.

(2) **Mucous Membranes.** — The *mucous membranes* line all those passages by which internal parts communicate with the exterior, and by which either matters are eliminated from the body or foreign substances taken into it. They are soft and velvety, and extremely vascular. The external surfaces of mucous membranes are attached to various other tissues; in the tongue, for example, to muscle; on cartilaginous parts, to perichondrium; in the cells of the ethmoid bone, in the frontal and sphenoidal sinuses, as well as in the tympanum, to periosteum; in the intestinal canal, it is connected with a firm submucous membrane, which on its exterior gives attachment to the fibres of the muscular coat. The mucous membranes line certain principal tracts—Gastro-Pulmonary and Genito-Urinary; the former being subdivided into the Digestive and Respiratory tracts. 1. The *Digestive* tract commences in the cavity of the mouth, from which prolongations pass into the ducts of the salivary glands. From the mouth it passes through the fauces, pharynx,

and œsophagus, to the stomach, and is thence continued along the whole tract of the intestinal canal to the termination of the rectum, being in its course arranged in the various folds and depressions already described, and prolonged into the ducts of the intestinal glands, the pancreas and liver, and into the gall-bladder. 2. The *Respiratory* tract includes the mucous membrane lining the cavity of the nose, and the various sinuses communicating with it, the lachrymal canal and sac, the conjunctiva of the eye and eyelids, and the prolongation which passes along the Eustachian tubes and lines the tympanum and the inner surface of the membrana tympani. Crossing the pharynx, and lining that part of it which is above the soft palate, the respiratory tract leads into the glottis, whence it is continued, through the larynx and trachea, to the bronchi and their divisions, which it lines as far as the branches of about $\frac{1}{50}$ of an inch in diameter, and continuous with it is a layer of delicate epithelial membrane which extends into the pulmonary cells. 3. The *Genito-urinary* tract, which lines the whole of the urinary passages, from their external orifice to the termination of the tubuli uriniferi of the kidneys, extends also into the organs of generation in both sexes, and into the ducts of the glands connected with them; and in the female becomes continuous with the serous membrane of the abdomen at the fimbriæ of the Fallopian tubes.

Structure.—Along each of the above tracts, and in different portions of each of them, the mucous membrane presents certain structural peculiarities adapted to the functions which each part has to discharge; yet in some essential characters mucous membrane is the same, from whatever part it is obtained. In all the principal and larger parts of the several tracts, it presents, as just remarked, an external layer of epithelium, situated upon *basement membrane*, and beneath this, a stratum of vascular tissue of variable thickness, containing lymphatic vessels and nerves which in different cases presents either out-growths in the form of papillæ and villi, or depressions or involutions in the form of glands. But in the prolongations of the tracts, where they pass into gland-ducts, these constituents are reduced in the finest branches of the ducts to the epithelium, the primary or basement-membrane, and the capillary blood-vessels spread over the outer surface of the latter in a single layer.

The primary or basement-membrane is a thin transparent layer, simple, homogeneous, or composed of endothelial cells. In the minuter divisions of the mucous membranes, and in the ducts of glands, it is the layer continuous and correspondent with this basement-membrane that forms the proper walls of the tubes. The cells also which, lining the larger and coarser mucous membranes, constitute their epithelium, are continuous with, and often similar to those which, lining the gland-ducts, are called *gland-cells.* No certain distinction can be drawn between the epithelium-cells of mucous membranes and gland-cells. It thus appears, that the tissues essential to the production of a secretion are, in their simplest form, a membrane, having on one surface blood-vessels, and on the other a layer of cells, which may be called either epithelium-cells or gland-cells.

Mucous Fluid: Mucus.—From all mucous membranes there is secreted either from the surface or from certain special glands, or from both, a more or less viscid, greyish, or semi-transparent fluid, of alkaline reaction and high specific gravity, named *mucus.* It mixes imperfectly with water, but, rapidly absorbing liquid, it swells considerably when water is added. Under the microscope it is found to contain epithelium and leucocytes. It is found to be made up, chemically, of a nitrogenous principle called *mucin* which forms its chief bulk, of a little albumen, of salts chiefly chlorides and phosphates, and water with traces of fats and extractives.

Secreting Glands.—The structure of the elementary portions of a secreting apparatus, namely epithelium, simple membrane, and blood-vessels having been already described in this and previous chapters, we may proceed to consider the manner in which they are arranged to form the varieties of *secreting glands.*

The secreting glands are the organs to which the function of *secretion* is more especially ascribed; for they appear to be occupied with it alone. They present, amid manifold diversities of form and composition, a general plan of structure, by which they are distinguished from all other textures of the body; especially, all contain, and appear constructed with particular regard to, the arrangement of the cells, which, as already expressed, both line their tubes or cavities as an epithelium, and elaborate, as secreting cells, the substances to be discharged from them. Glands are provided also with lymphatic vessels and nerves. The distribution of the former is not peculiar, and need not be here considered. Nerve-fibres are distributed both to the blood-vessels of the gland and to its ducts; and, in some glands, to the secreting cells also (p. 282).

Varieties.—1. The *simple tubule*, or *tubular gland* (A, fig. 220), examples of which are furnished by some mucous glands, the follicles of Lieberkühn (fig. 186), and the tubular glands of the stomach. These appear to be simple tubular depressions of the mucous membrane, the wall of which is formed of primary membrane, and is lined with secreting cells arranged as an epithelium. To the same class may be referred the elongated and tortuous sudoriferous glands.

The compound *tubular glands* (D, fig. 220) form another division. These consist of main gland-tubes, which divide and sub-divide. Each gland may consist of the subdivisions of one or more main tubes. The ultimate sub-divisions of the tubes are generally highly convoluted. They are formed of a basement-membrane, lined by epithelium of various forms. The larger tubes may have an outside coating of fibrous, areolar, or muscular tissue. The kidney, testis, salivary glands, pancreas, Brunner's glands with the lachrymal and mammary glands, and some mucous glands are examples of this type, but present more or less marked variations among themselves.

2. The *aggregate* or *racemose glands*, in which a number of vesicles or *acini* are arranged in groups or lobules (C, fig. 220). The Meibomian follicles are examples of this kind of gland.

These various organs differ from each other only in secondary points of structure; such as, chiefly, the arrangement of their excretory ducts, the grouping of the *acini* and lobules, their connection by areolar tissue, and supply of blood vessels. The acini commonly appear to be formed by a kind of fusion of the walls of several vesicles, which thus combine to form one cavity lined or filled with secreting cells which also occupy recesses from the main cavity. The smallest branches of the gland-ducts sometimes open into the centres of these cavities; sometimes the acini are clustered round the extremities, or by the sides of the ducts: but, whatever secondary arrangement there may be, all have the same essential character of rounded groups of vesicles containing gland-cells, and opening by a common central cavity into minute ducts, which ducts in the large glands converge and unite to form larger and larger branches, and at length by one common trunk, open on a free surface of membrane.

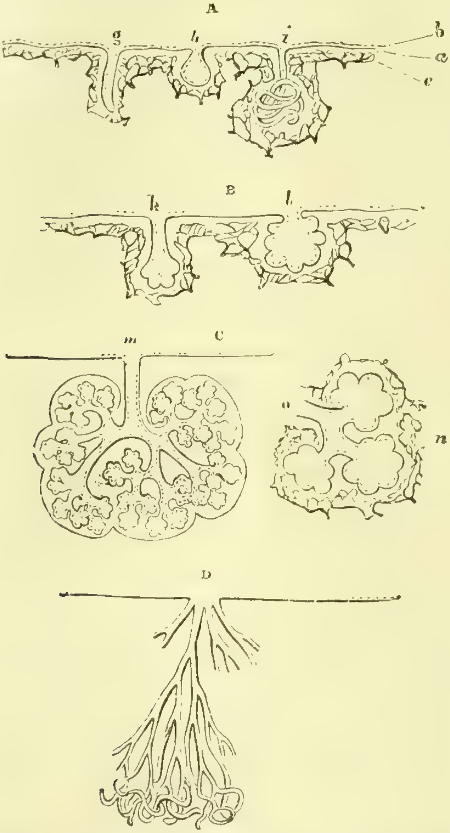

Fig. 220.—*Plans of extension of secreting membrane by inversion or recession in form of cavities.* A, simple glands, viz. *g*, straight tube; *h*, sac; *i*, coiled tube. B, multilocular crypts; *k*, of tubular form; *l*, saccular. C, racemose, or saccular compound gland; *m*, entire gland, showing branched duct and lobular structure; *n*, a lobule, detached with *o*, branch of duct proceeding from it. D, compound tubular gland (Sharpey).

Among these varieties of structure, all the secreting glands are alike in some essential points, besides those which they have in common with all truly secreting structures. They agree in presenting a large extent of secreting surface within a comparatively small space; in the circumstance that while one end of the gland-duct opens on a free surface, the opposite end is always closed, having no direct communication with blood-vessels, or any other canal; and in an uniform arrangement of capillary blood-vessels, ramifying and forming a network around the walls and in the interstices of the ducts and acini.

Process of Secretion.—In secretion two distinct processes are concerned which may be spoken of as I. *Physical*, and II. *Chemical*.

1. *Physical processes.*—These are such as can be closely imitated in the laboratory, inasmuch as they consist in the operation of well-known physical laws: they are—

(*a*) Filtration. (*b*) Diffusion.

(*a*) *Filtration* is simply the passage of a fluid through a porous membrane under the influence of pressure. If two fluids be separated by a porous membrane, and the pressure on one side is greater than on the other, it is evident that in the absence of counteracting osmotic influences (see below) there will be a filtration through the membrane until the pressure on the two sides is equalized. Of course there may only be fluid on one side of the membrane, as in the ordinary process of filtering through blotting-paper, and then the filtration will continue as long as the pressure (in this case, the weight of the fluid) is sufficient to force it through the pores of the filter. The necessary inequality of pressure may be obtained either by diminishing it on one side, as in the case of cupping; or increasing it on the other, as in the case of the increased blood-pressure and consequent increased flow of urine resulting from copious drinking. By filtration, not merely water, but various salts in solution may transude from the blood vessels. It seems probable that some fluids, such as the secretions of serous membranes, are simply exudations or oozings (filtration) from the blood-vessels, whose qualities are determined by those of the liquor sanguinis, while the quantities are liable to variation, and are chiefly dependent upon the blood-pressure.

(*b*) *Diffusion* is the passage of fluids through a moist animal membrane independent of pressure, and sometimes actually in opposition to it. There must always be in this process two fluids differing in composition, one or both possessing an affinity for the intervening membrane, and the fluids capable of being mixed one with the other; the osmotic current continuing in each direction (when both fluids have an affinity for the membrane) until the chemical composition of the fluid on each side of the septum becomes the same.

2. *Chemical processes.*—These constitute the process of *secretion* properly so called as distinguished from mere transudation spoken of above. In the *chemical* process of *secretion* various materials which do not exist as such in the blood are elaborated by the agency of the gland-cells from the blood, or, to speak more accurately, from the *plasma* which exudes from the blood-vessels into the interstices of the gland-textures.

The best evidence for this view is: 1*st.* That cells and nuclei are constituents of all glands, however diverse their outer forms and other characters, and are in all glands placed on the surface or in the cavity whence the secretion is poured. 2*nd.* That many secretions which are visible with the microscope may be seen in the cells of their glands before they are discharged. Thus, bile may be often discerned by its yellow tinge in the gland-cells of the liver; spermatozoids in the cells of the tubules of the testicles; granules of uric acid in those of the kidneys (of fish); fatty particles, like those of milk, in the cells of the mammary gland.

Secreting cells, like the cells or other elements of any other organ, appear to develop, grow, and attain their individual perfection by appropriating nutriment from the fluid exuded by adjacent blood-vessels and elaborating it, so that it shall form part of their own substance. In this perfected state, the cells subsist for some brief time, and when that period is over they appear to dissolve, wholly or in part, and yield their contents to the peculiar material of the secretion. And this appears to be the case in every part of the gland that contains the appropriate gland-cells; therefore not in the extremities of the ducts or in the acini alone, but in great part of their length.

We have described elsewhere the changes which have been noticed from actual experiment in the cells of the salivary glands, pancreas, and peptic gland (pp. 289, 321, 329).

Discharge of Secretions from glands may either take place as soon as they are formed; or the secretion may be long retained within the gland or its ducts. The former is the case with the sweat glands. But the secretions of those glands whose activity of function is only occasional are usually retained in the cells in an undeveloped form during the periods of the gland's inaction. And there are glands which are like both these classes, such as the lachrymal, which constantly secrete small portions of fluid, and on occasions of greater excitement discharge it more abundantly.

When discharged into the ducts, the further course of secretions is affected partly by the pressure from behind; the fresh quantities of secretion propelling those that were formed before. In the larger ducts, its propulsion is assisted by the contraction of their walls. All the larger ducts, such as the ureter and common bile-duct, possess in their coats plain muscular fibres; they contract when irritated, and sometimes manifest peristaltic movements. Rhythmic contractions in the pancreatic and bile-ducts have been observed, and also in the ureters and vasa deferentia. It is probable that the contractile power extends along the ducts to a considerable distance within the substance of the glands whose secretions can be rapidly expelled. Saliva and milk, for instance, are sometimes ejected with much force; doubtless by the energetic and simultaneous contraction of many of the ducts of their respective glands.

Circumstances Influencing Secretion.—Amongst the principal conditions which influence secretion are (1) variations in the quantity of blood, (2) in the quantity of the peculiar materials for any secretion that it may contain, and (3) in conditions of the nerves of the glands.

(1.) *An increase in the quantity of blood traversing a gland*, as in nearly all the instances before quoted, coincides generally with an augmentation of its secretion. Thus, the mucous membrane of the stomach becomes florid when, on the introduction of food, its glands begin to secrete; the mammary gland becomes much more vascular during lactation; and all circumstances which give rise to an increase in the quantity of material secreted by an organ produce, coincidently, an increased supply of blood; but we have seen that a discharge of saliva may occur under extraordinary circumstances, without increase of blood-supply (p. 287), and so it may be inferred that this condition of increased blood-supply is not absolutely essential.

(2.) When the blood contains more than usual of the materials which the glands are designed to separate or elaborate. Thus, when an excess of nitrogenous waste is in the blood, whether from excessive exercise, or from destruction of one kidney, a healthy kidney will excrete more urea than it did before.

(3.) *Influence of the Nervous System on Secretion.*—The process of secretion is largely influenced by the condition of the nervous system. The exact mode in which the influence is exhibited must still be regarded as somewhat obscure. In part, it exerts its influence by increasing or diminishing the quantity of blood supplied to the secreting gland, in virtue of the power which it exercises over the contractility of the smaller blood vessels; while it also has a more direct influence, as was demonstrated at length in the case of the submaxillary gland, upon the secreting cells themselves; this may be called *trophic* influence. Its influence over secretion, as well as over other functions of the body, may be excited by causes acting directly upon the nervous centres, upon the nerves going to the secreting organ, or upon the nerves of other parts. In the latter case, a reflex action is produced: thus the impression produced upon the nervous centres by the contact of food in the mouth, is reflected upon the nerves supplying the salivary glands, and produces, through these, a more abundant secretion of saliva (p. 286).

Through the nerves, various conditions of the brain also influence the secretions. Thus, the thought of food may be sufficient to excite an abundant flow of saliva. And, probably, it is the mental state which excites the abundant secretion of urine in hysterical paroxysms, as well as the perspirations and, occasionally, diarrhœa, which ensue under the influence of terror, and the tears excited by sorrow or excess of joy. The quality of a secretion may also be affected by the mind; as in the cases in which, through grief or passion the secretion of milk is altered, and is sometimes so changed as to produce irritation in the alimentary canal of the child, or even death (Carpenter).

Relations between the Secretions.—The secretions of some of the glands seem to bear a certain relation or antagonism to each other, by which an increased activity of one is usually followed by diminished activity of one or more of the others; and a deranged condition of one is apt to entail a disordered state in the others. Such relations appear to exist among the various mucous membranes; and the close relation between the secretion of the kidney and that of the skin is a subject of constant observation.

The Mammary Glands and their Secretion: Milk.

Structure.—The mammary glands are composed of large divisions or lobes, and these are again divisible into lobules,—the lobules being composed of the convoluted subdivision of ducts (alveoli). The lobes and lobules are bound together by areolar tissue; penetrating between the lobes, and covering the general surface of the gland, with the exception of the nipple, is a considerable quantity of yellow fat, itself lobulated by sheaths and processes of tough areolar tissue (fig. 221) connected both with the skin in front and the gland behind; the same bond of connection extending also from the under surface of the gland to the sheathing connective

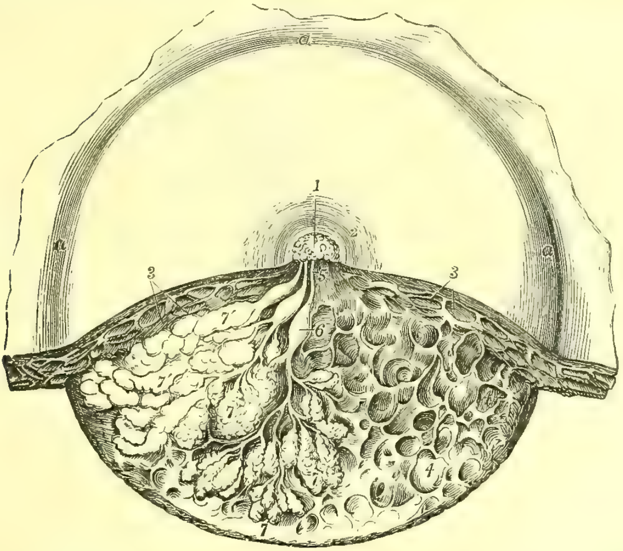

Fig. 221.—*Dissection of the lower half of the female mamma* during the period of lactation. ⅔.—In the left-hand side of the dissected part the glandular lobes are exposed and partially unravelled; and on the right-hand side, the glandular substance has been removed to show the reticular loculi of the connective-tissue in which the glandular lobules are placed: 1, upper part of the mamilla or nipple; 2, areola; 3, subcutaneous masses of fat; 4, reticular loculi of the connective-tissue which support the glandular substance and contain the fatty masses; 5, one of three lactiferous ducts shown passing towards the mamilla where they open; 6, one of the sinus lactei or reservoirs; 7, some of the glandular lobules which have been unravelled; 7′, others massed together (Luschka).

tissue of the great pectoral muscle on which it lies. The main ducts of the gland, fifteen to twenty in number, called the *lactiferous* or *galactophorous* ducts, are formed by the union of the smaller (lobular) ducts, and open by small separate orifices through the nipple. At the points of junction of lobular ducts to form lactiferous ducts, and just before these enter the base of the nipple, the ducts are dilated (6, fig. 221); and, during lactation, the period of active secretion by the gland, the dilatations form reservoirs for the milk, which collects in them and distends them. The walls of the gland-ducts are formed of areolar and elastic with some muscular tissue, and are lined internally by short columnar and near the nipple by squamous epithelium. The alveoli consist of a membrana propria of flattened endothelial cells lined by low columnar epithelium, and are filled with fat globules.

The nipple, which contains the terminations of the lactiferous ducts, is composed also of areolar tissue, and contains unstriped muscular fibres. Blood-vessels are also freely supplied to it, so as to give it a species of erectile structure. On its surface are very sensitive papillæ; and around it is a small area or *areola* of pink or dark-tinted skin, on which are to be seen small projections formed by minute secreting glands.

Blood-vessels, nerves, and lymphatics are plentifully supplied to the mammary glands; the calibre of the blood-vessels, as well as the size of the glands, varying very greatly under certain conditions, especially those of pregnancy and lactation.

Changes in the Glands at certain Periods.—The minute changes which occur in the mammary gland during its periods of evolution (pregnancy), and involution (when lactation has ceased), are the following:—

The most favourable period for observing the epithelium of the mammary gland fully developed is shortly before the end of pregnancy. At this period the acini which form the lobules of the gland, are found to be lined with a mosaic of polyhedral epithelial cells (fig. 222), and supported by a connective tissue stroma.

The rapid formation of milk during *lactation* results from a fatty metamorphosis of the epithelial cells: "The secretion may be said to be produced by a transformation of the substance of successive generations of epithelial cells, and in the state of full activity this transformation is so complete that it may be called a deliquescence" (Creighton).

In the earlier days of lactation, epithelial cells partially transformed are discharged in the secretion: these are termed "colostrum corpuscles," but later on the cells are completely transformed before the secretion is discharged.

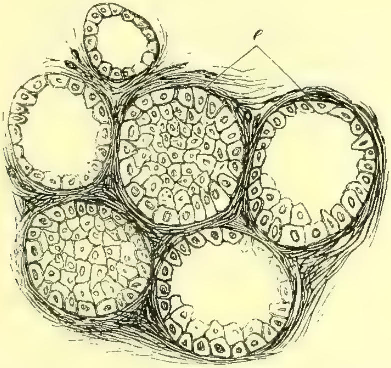

Fig. 222.—*Section of mammary gland of rabbit near the end of pregnancy*, showing six acini. *e*, epithelial cells of a polyhedral or short columnar form, with which the acini are packed. × 200. (Schofield.)

After the end of lactation, the mamma gradually returns to its original size (*involution*). The acini, in the early stages of involution, are lined with cells in all degrees of vacuolation (fig. 223). As involution proceeds the acini diminish considerably in size, and at length, instead of a mosaic of lining epithelial cells (twenty to thirty in each acinus), we have five or six nuclei (some with no surrounding protoplasm) lying in an irregular heap within the acinus. During the later stages of involution, large yellow granular cells are to be seen. As the acini diminish in size, the connective tissue and fatty matter between them increase, and in some animals, when the gland is completely inactive, it is found to consist of a thin film of glandular tissue overlying a thick cushion of fat. Many of the products of waste are carried off by the lymphatics.

During *pregnancy* the mammary glands undergo changes (*evolution*) which are readily observable. They enlarge, become harder and more distinctly lobulated: the veins on the surface become more prominent. The areola becomes enlarged and dusky, with projecting papillæ; the nipple too becomes more prominent, and milk can be squeezed from the orifices of the ducts. This is a very gradual process, which commences about the time of conception,

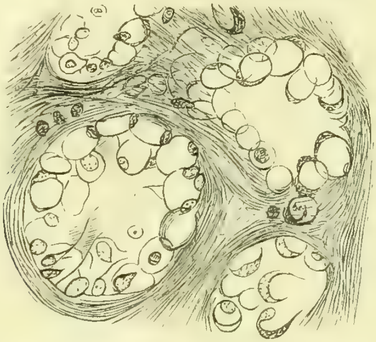

Fig. 223.—*Section of mammary gland of ewe shortly after the end of lactation*, showing parts of four acini, which contain numerous epithelial cells undergoing vacuolation *in situ*; they very closely resemble young fat-cells, and are in fact just like "Colostrum corpuscles." × 300. (Creighton.)

and progresses steadily during the whole period of gestation. The acini enlarge, and a series of changes occur, exactly the reverse of those just described under the head of Involution.

The Mammary Secretion: Milk.

Under the microscope, milk is found to contain a number of globules of various sizes (fig. 224), the majority about $\frac{1}{10000}$ of an inch in diameter. They are composed of oily matter, probably coated by a fine layer of albuminous material, and are called *milk-globules;* while, accompanying these, are numerous minute particles, both oily and albuminous, which exhibit ordinary molecular movements. The milk which is secreted in the first few days after parturition, and which is called the *colostrum,* differs from ordinary milk in containing a larger quantity of solid matter; and under the microscope are to be seen certain granular masses called *colostrum-corpuscles.* These, which appear to be small masses of albuminous and oily matter, are probably secreting cells of the gland, either in a state of fatty degeneration, or old cells which in their attempt at secretion under the new circumstances of active need of milk, are filled with oily matter; which, however, being unable to discharge, they are themselves shed bodily to make room for their successors. Colostrum-corpuscles have been seen to exhibit contractile movements and to squeeze out drops of oil from their interior (Stricker).

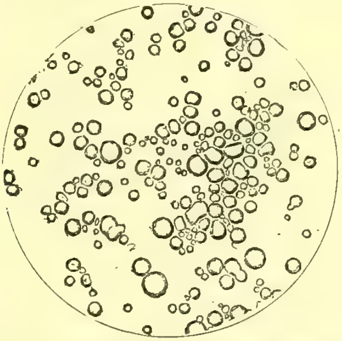

Fig. 224.—*Globules and molecules of Cow's milk.* × 400.

Chemical Composition.—Milk is in reality an emulsion consisting of numberless little globules of fat, coated with a thin layer of albuminous matter, floating in a large quantity of water which contains in solution casein, serum-albumin, milk-sugar (lactose), and several salts. Its percentage composition has been already mentioned, but may be here repeated. Its reaction is alkaline: its specific gravity about 1030.

Table of the Chemical Composition of Milk.

	Human.	Cows.
Water	890	858
Solids	110	142
	1000	1000
Proteids, including Casein and Serum-Albumin	35	68
Fats or Butter	25	38
Sugar (with extractives)	48	30
Salts	2	6
	110	142

When milk is allowed to stand, the fat globules, being the lightest portion, rise to the top, forming *cream*. If a little acetic acid be added to a drop of milk under the microscope, the albuminous film coating the oil drops is dissolved, and they run together into larger drops. The same result is produced by the process of *churning*, the effect of which is to break up the albuminous coating of the oil drops: they then coalesce to form *butter*.

Curdling of Milk.—If milk be allowed to stand for some time, its reaction becomes acid: in popular language it "turns sour." This change appears to be due to the conversion of the milk-sugar into lactic acid, which causes the precipitation of the casein (curdling): the curd contains the fat globules: the remaining fluid (whey) consists of water holding in solution albumin, milk-sugar and certain salts. The same effect is produced in the manufacture of cheese, which is really casein coagulated by the agency of rennet (p. 307). When milk is boiled, a scum of serum-albumin forms on the surface.

Curdling Ferments.—The effect of the ferments of the gastric, pancreatic, and intestinal juices in curdling milk (*curdling ferments*) has already been mentioned in the Chapter on Digestion.

The salts of milk are chlorides, sulphates, phosphates, and carbonates of potassium, sodium, calcium.

CHAPTER XII.

THE SKIN AND ITS FUNCTIONS.

THE skin serves—(1), as an external integument for the protection of the deeper tissues, and (2), as a sensitive organ in the exercise of touch; it is also (3), an important excretory, and (4), an absorbing organ; while it plays an important part in (5) the regulation of the temperature of the body.

Structure of the Skin.—The skin consists, principally, of a vascular tissue, named the *corium*, *derma*, or *cutis vera*, and an external covering of epithelium termed the *cuticle* or *epidermis*. Within and beneath the corium are imbedded several organs with special function, namely *sudoriferous* glands, *sebaceous* glands, and *hair follicles;* and on its surface are sensitive *papillæ.* The so-called appendages of the skin—the *hair* and *nails*—are modifications of the epidermis.

Epidermis.—The epidermis is composed of several strata of cells of various shapes, and closely resembles in its structure that which lines the mouth. The following four layers may be distinguished. 1. *Stratum corneum* (fig. 225, *a*), consisting of many superposed layers of horny scales. The different thickness of the epidermis in different regions of the body is chiefly due to variations in the thickness of this layer; *e.g.*, on the horny parts of the palms of the hands and soles of the feet it is of great thickness. The stratum corneum of the buccal epithelium chiefly differs from that of the epidermis in the fact that nuclei are to be distinguished in some of the cells even of its most superficial layers.

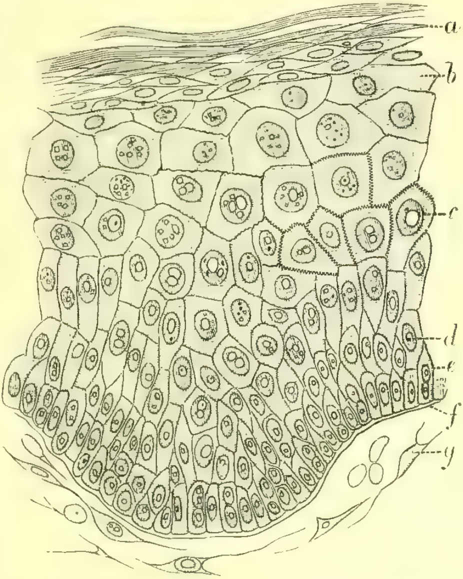

Fig. 225.—*Vertical section of the epidermis of the prepuce.* *a*, stratum corneum, of very few layers, the stratum lucidum and stratum granulosum not being distinctly represented; *b*, *c*, *d*, and *e*, the layers of the stratum Malpighi, a certain number of the cells in layers *d* and *e* showing signs of segmentation; layer *c* consists chiefly of prickle or ridge and furrow cells; *f*, basement membrane; *g*, cells in cutis vera. (Cadiat.)

2. *Stratum lucidum,* a bright homogeneous membrane consisting of squamous cells closely arranged, in some of which a nucleus can be seen.

3. *Stratum granulosum,* consisting of one layer of flattened cells which appear fusiform in vertical section: they are distinctly nucleated, and a number of granules extend from the nucleus to the margins of the cell.

4. *Stratum Malpighii* or *Rete mucosum*, which consists of many strata. The deepest cells, placed immediately above the cutis vera, are columnar with oval nuclei: this layer of columnar cells is succeeded by a number of layers of more or less polyhedral cells with spherical nuclei; the cells of the more superficial layers are considerably flattened. The deeper surface of the rete mucosum is accurately adapted to the papillæ of the true skin, being, as it were, moulded on them. It is very constant in thickness in all parts of the skin. The cells of the middle layers of the stratum Malpighii are almost all connected by processes, and thus form "prickle cells" (p. 24). The pigment of the skin, the varying quantity of which causes the various tints observed in different individuals and different races, is contained in the deeper cells of the rete mucosum; the pigmented cells as they approach the free surface gradually losing their colour. Epidermis maintains its thickness in spite of the constant wear and tear to which it is subjected. The columnar cells of the deepest layer of the "rete mucosum" elongate, and their nuclei divide into two (fig. 225, *e*). Lastly the upper part of the cell divides from the lower; thus from a long columnar cell are produced a polyhedral and a short columnar cell: the latter elongates and the process is repeated. The polyhedral cells thus formed are pushed up towards the free surface by the production of fresh ones beneath them, and become flattened from pressure: they also become gradually horny by evaporation and transformation of their protoplasm into keratin, till at last by rubbing they are detached as dry horny scales at the free surface. There is thus a constant production of fresh cells in the deeper layers, and a constant throwing off of old ones

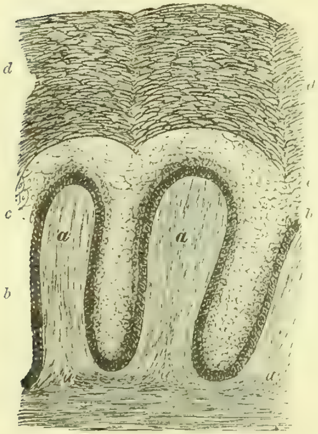

Fig. 226.—*Vertical section of skin of the negro.* *a*, *a*. Cutaneous papillæ. *b*. Undermost and dark-coloured layer of oblong vertical epidermis-cells. *c*. Stratum Malpighii. *d*. Superficial layers, including stratum corneum, stratum lucidum, and stratum granulosum, the last two not differentiated in fig. × 250 (Sharpey.)

from the free surface. When these two processes are accurately balanced, the epidermis maintains its thickness. When, by intermittent pressure a more active cell-growth is stimulated, the production of cells exceeds their waste and the epidermis increases in thickness, as we see in the horny hands of the labourer.

The thickness of the epidermis on different portions of the skin is directly proportioned to the friction, pressure, and other sources of injury to which it is exposed; for it serves as well to protect the sensitive and vascular cutis from injury from without, as to limit the evaporation of fluid from the blood-vessels. The adaptation of the epidermis to the latter purposes may be well shown by exposing to the air two dead hands or feet, of which one has its epidermis perfect, and the other is deprived of it; in a day, the skin of the latter will become brown, dry, and horn-like, while that of the former will almost retain its natural moisture.

Cutis vera.—The *corium* or *cutis*, which rests upon a layer of adipose and cellular tissue of varying thickness, is a dense and tough, but yielding and highly elastic structure, composed of fasciculi of fibro-cellular tissue, interwoven in all directions, and forming, by their interlacements, numerous spaces or areolæ. These areolæ are large in the deeper layers of the cutis, and are there usually filled with little masses of fat (fig. 228): but, in the superficial parts, they are small or entirely obliterated. Plain muscular fibre is also abundantly present.

Papillæ.—The papillæ are conical elevations of the cutis vera, with a single or divided free extremity, more prominent and more densely set at some parts than at others (figs. 227 and 230). The parts on which they are most abundant and most prominent, are

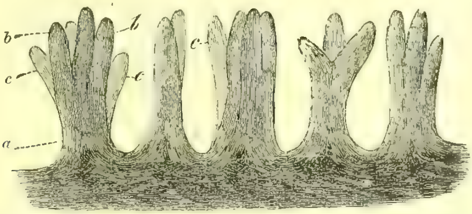

Fig. 227.—*Compound papillæ from the palm of the hand;* *a*, basis of a papilla; *b*, *b*, divisions or branches of the same; *c*, *c*, branches belonging to papillæ, of which the bases are hidden from view. × 60 (Kölilker).

the palmar surface of the hands and fingers, and the soles of the feet—parts, therefore, in which the sense of touch is most acute. On these parts they are disposed in double rows, in parallel curved lines, separated from each other by depressions. Thus they may be seen easily on the palm, whereon each raised line is composed of a double row of papillæ, and is intersected by short transverse lines or furrows corresponding with the interspaces between the successive pairs of papillæ. Over other parts of the skin they are more or less thinly scattered, and are scarcely elevated above the surface. Their average length is about $\frac{1}{100}$ of an inch, and at their base they measure about $\frac{1}{250}$ of an inch in diameter. Each papilla is abundantly supplied with blood, receiving from the vascular plexus in the cutis one or more minute arterial twigs, which divide into capillary loops in its

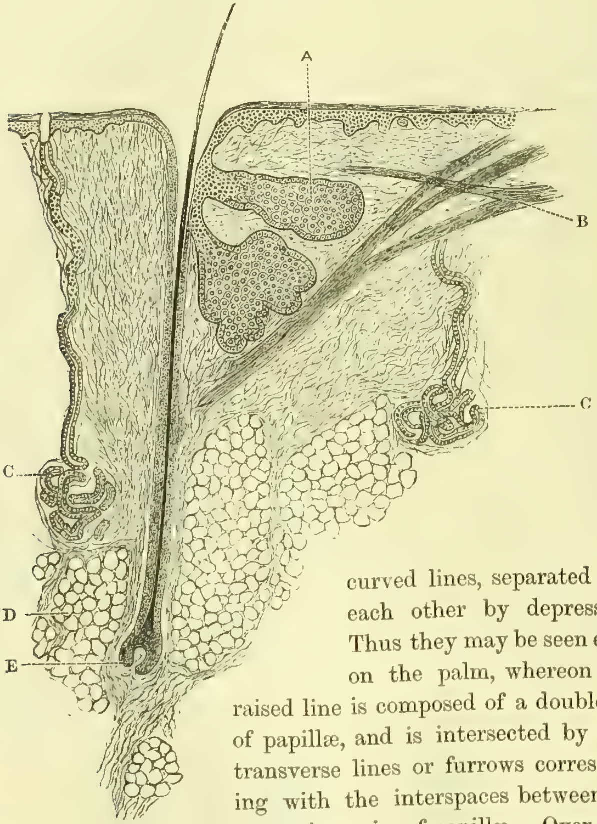

Fig. 228.—*Vertical section of skin.* A. Sebaceous gland opening into hair-follicle. B. Muscular fibres. C. Sudoriferous or sweat-gland. D. Subcutaneous fat. E. Fundus of hair-follicle, with hair-papillæ. (Klein and Noble Smith.)

substance, and then reunite into a minute vein, which passes out at its base. The abundant supply of blood which the papillæ thus receive explains the turgescence or kind of erection which they undergo when the circulation through the skin is active. The majority, but not all, of the papillæ contain also one or more terminal nerve-fibres, from the ultimate ramifications of the cutaneous plexus, on which their exquisite sensibility depends.

Nerve-terminations.—In some parts, especially those in which the sense of touch is highly developed, as, for example, the palm of the hand and the lips, the nerve-fibres appear to terminate, in many of the papillæ, by one or more free ends in the substance of an oval-shaped body, occupying the principal part of the interior of the papilla, and termed a *touch-corpuscle* (fig. 229). The nature of this body is obscure. Some regard it as little else than a mass of fibrous or connective tissue, surrounded by elastic fibres, and formed, according to Huxley, by an increased development of the primitive sheaths of the nerve-fibres, entering the papillæ. Others, however, believe that, instead of thus consisting of a homogeneous mass of connective tissue, they are special and peculiar bodies of laminated structure, directly concerned in the sense of touch. They do not occur in

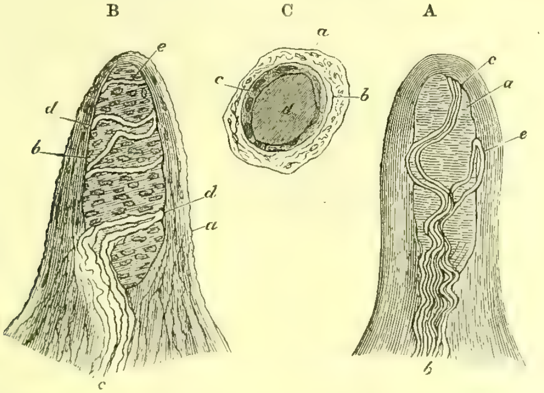

Fig. 229.—*Papillæ from the skin of the hand*, freed from the cuticle and exhibiting tactile corpuscles. A. Simple papilla with four nerve-fibres : *a*, tactile corpuscles ; *b*, nerves. B. Papilla treated with acetic acid ; *a*, cortical layer with cells and fine elastic filaments ; *b*, tactile corpuscle with transverse nuclei ; *c*, entering nerve with neurilemma or perineurium ; *d*, nerve-fibres winding round the corpuscle. C. Papilla viewed from above so as to appear as a cross section : *a*, cortical layer ; *b*, nerve-fibre ; *c*, sheath of the tactile corpuscle containing nuclei ; *d*, core. × 350. (Kölliker.)

all the papillæ of the parts where they are found, and, as a rule, in the papillæ in which they are present there are no blood-vessels. Since these peculiar bodies in which the nerve-fibres end are only met with in the papillæ of highly sensitive parts, it may be inferred that they are specially concerned in the sense of touch, yet their absence from the papillæ of other tactile parts shows that they are not essential to this sense.

Closely allied in structure to the touch-corpuscles are some little bodies called *end-bulbs*, about $\frac{1}{600}$ inch in diameter (Krause). They are generally oval or spheroidal, and composed externally of a coat of connective tissue enclosing a softer matter, in which the extremity of a nerve terminates. These bodies have been found chiefly in the lips, tongue, palate, and the skin of the glans penis (fig. 230).

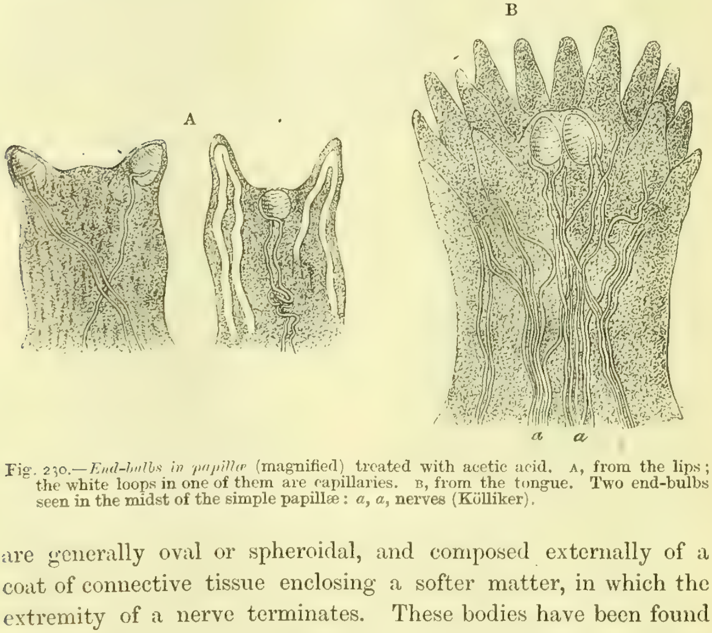

Fig. 230.—*End-bulbs in papillæ* (magnified) treated with acetic acid. A, from the lips; the white loops in one of them are capillaries. B, from the tongue. Two end-bulbs seen in the midst of the simple papillæ: *a*, *a*, nerves (Kölliker).

Glands of the Skin.—The skin possesses glands of two kinds; (*a*) Sudoriferous, or Sweat Glands; (*b*) Sebaceous Glands.

(*a*) *Sudoriferous, or Sweat Glands.*—Each of these glands consists of a small lobular mass, formed of a coil of tubular gland-duct, surrounded by blood-vessels and embedded in the subcutaneous adipose tissue (fig. 228, C.). From this mass, the duct ascends, for a short distance in a spiral manner through the deeper part of the cutis, then passing straight, and then sometimes again becoming spiral, it passes through the cuticle and opens by an oblique valve-like aperture. In the parts where the epidermis is thin, the ducts themselves are thinner and more nearly straight in their course (fig. 228). The duct, which maintains nearly the same diameter throughout, is lined with a layer of columnar epithelium (fig. 231) continuous with the epidermis; while the part which passes through the epidermis is composed of the latter structure only; the cells which immediately form the boundary of the canal in this part being somewhat differently arranged from those of the adjacent cuticle.

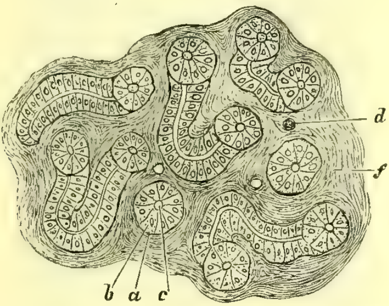

Fig. 231.—*Glomeruli of sudoriferous gland*, divided in various directions. *a*, sheath of the gland; *b*, columnar epithelial lining of gland tube; *c*, lumen of tube; *d*, divided blood-vessel; *f*, loose connective-tissue, forming a capsule to the gland (Biesiadecki).

The sudoriferous glands are abundantly distributed over the whole surface of the body; but are especially numerous, as well as very large, in the skin of the palm of the hand, and of the sole of the foot. The glands by which the peculiar odorous matter of the axillæ is secreted form a nearly complete layer under the cutis, and are like the ordinary sudoriferous glands, except in being larger and having very short ducts.

The peculiar bitter yellow substance secreted by the skin of the external auditory passage is named *cerumen*, and the glands themselves *ceruminous* glands; but they do not much differ in structure from the ordinary sudoriferous glands.

(*b*) *Sebaceous Glands.*—The sebaceous glands (fig. 232), like the sudoriferous glands, are abundantly distributed over most parts of the body. They are most numerous in parts largely supplied with hair, as the scalp and face, and are thickly distributed about the entrances of the various passages into the body, as the anus, nose, lips, and external ear. They are entirely absent from the palmar surface of the hand and the plantar surfaces of the feet. They are minutely lobulated glands composed of an aggregate of small tubes or sacculi filled with opaque white substances, like soft ointment. Minute capillary vessels overspread them; and their ducts open either on the surface of the skin, close to a hair, or, which is more usual, directly into the follicle of the hair. In the latter case, there are generally two or more glands to each hair (fig. 228).

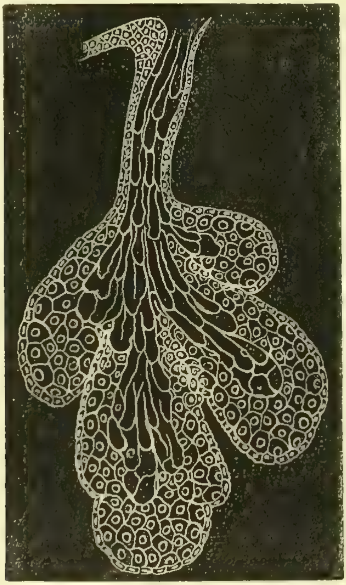

Fig. 232.—*Sebaceous gland from human skin* (Klein and Noble Smith).

Hair.—A hair is produced by a peculiar growth and modification of the epidermis. Externally it is covered by a layer of fine scales closely imbricated, or overlapping like the tiles of a house, but with the free edges turned upwards (fig. 233, A). It is called the *cuticle* of the hair. Beneath this is a much thicker layer of elongated horny cells, closely packed together so as to resemble a fibrous structure. This, very commonly, in the human subject, occupies the whole of the inside of the hair; but in some

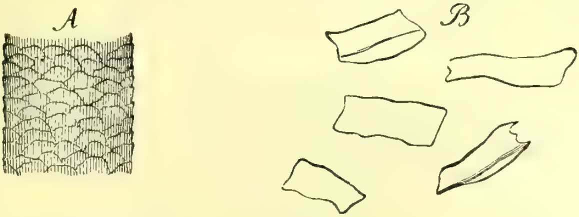

Fig. 233.—*Surface of a white hair*, magnified 160 diameters. The wave lines mark the upper or free edges of the cortical scales. *B*, separated scales, magnified 350 diameters (Kölliker).

cases there is left a small central space filled by a substance called

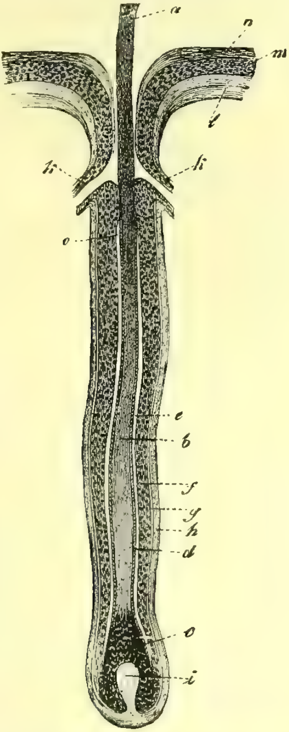

Fig. 234.—*Medium-sized hair in its follicle.* *a*, stem cut short; *b*, root; *c*, knob; *d*, hair cuticle; *e*, internal, and *f*, external root-sheath; *g*, *h*, dermic coat of follicle; *i*, papilla; *k*, *k*, ducts of sebaceous glands; *l*, corium; *m*, mucous layer of epidermis; *o*, upper limit of internal root sheath × 50 (Kölliker). See also fig. 235.

the *medulla* or *pith*, composed of small collections of irregularly shaped cells, containing sometimes pigment granules or fat, but mostly air.

The follicle, in which the root of each hair is contained (fig. 235), forms a tubular depression from the surface of the skin,—descending into the subcutaneous fat, generally to a greater depth than the sudoriferous glands, and at its deepest part enlarging in a bulbous form, and often curving from its previous rectilinear course. It is lined throughout by cells of epithelium, continuous with those of the epidermis, and its walls are formed of pellucid membrane, which commonly, in the follicles of the largest hairs, has the structure of vascular fibrous tissue. At the bottom of the follicle is a small papilla, or projection of true skin, and it is by the production and out-growth of epidermal cells from the surface of this papilla that the hair is formed. The inner wall of the follicle is lined by epidermal cells continuous with those covering the general surface of the skin; as if indeed the follicle had been formed by a simple thrusting in of the surface of the integument (fig. 234). This epidermal lining of the hair-

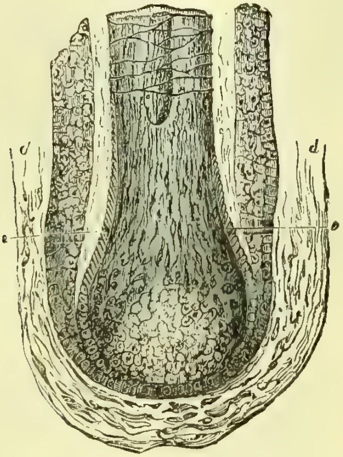

Fig. 235.—*Magnified view of the root of a hair.* *a*, stem or shaft of hair cut across; *b*, inner, and *c*, outer layer of the epidermal lining of the hair-follicle, called also the inner and outer root-sheath; *d*, dermal or external coat of the hair-follicle, shown in part, *e*, imbricated scales about to form a cortical layer on the surface of the hair. The adjacent cuticle of the root-sheath is not represented, and the papilla is hidden in the lower part of the knob where that is represented lighter (Kohlrausch).

follicle, or *root-sheath* of the hair, is composed of two layers, the inner one of which is so moulded on the imbricated scaly cuticle of the hair, that its inner surface becomes imbricated also, but of course in the opposite direction. When a hair is pulled out, the inner layer of the *root-sheath* and part of the outer layer also are commonly pulled out with it.

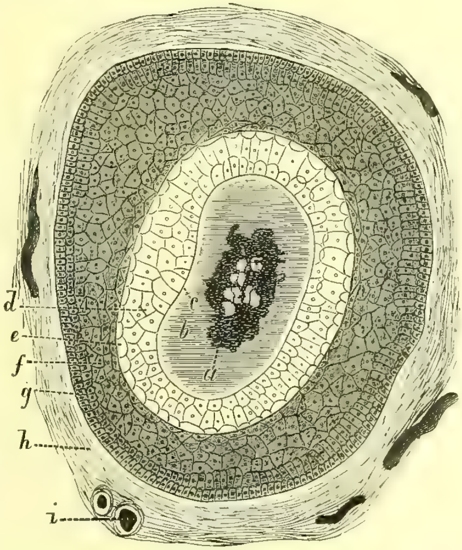

Fig. 236.—*Transverse section of a hair and hair-follicle* made below the opening of the sebaceous gland. *a*, medulla or pith of the hair; *b*, fibrous layer or cortex; *c*, cuticle; *d*, Huxley's layer, *e*, Henle's layer of internal root-sheath; *f* and *g*, layers of external root-sheath, outside of *g* is a light layer, or "glassy membrane," which is equivalent to the basement membrane; *h*, fibrous coat of hair sac; *i*, vessels. (Cadiat.)

Nails. — A *nail*, like a hair, is a peculiar arrangement of epidermal cells, the undermost of which, like those of the general surface of the integument, are rounded or elongated, while the superficial are flattened, and of more horny consistence. That specially modified portion of the corium, or true skin, by which the nail is secreted, is called the *matrix*.

The back edge of the nail, or the *root* as it is termed, is received into a shallow crescentic groove in the *matrix*, while the front part is free and projects beyond the extremity of the digit. The intermediate portion of the nail rests by its broad under-surface on the front part of the matrix, which is here called the *bed* of the nail. This part of the matrix is not uniformly smooth on the surface, but is raised in the form of longitudinal and nearly parallel ridges or laminæ, on which are moulded the epidermal cells of which the nail is made up (fig. 237).

The growth of the nail, like that of the hair, or of the epidermis generally, is effected by a constant production of cells from beneath and behind, to take the place of those which are worn or cut away. Inasmuch, however, as the posterior edge of the nail, from its being lodged in a groove of the skin, cannot grow backwards, on additions being made to it, so easily as it can pass in the opposite direction, any growth at its hinder part pushes the whole forwards. At the same time fresh cells are added to its under surface, and thus each portion of the nail becomes gradually thicker as it moves to the front, until, projecting beyond the surface of the matrix, it can receive no fresh addition from beneath, and is simply moved forwards by the growth at its root, to be at last worn away or cut off.

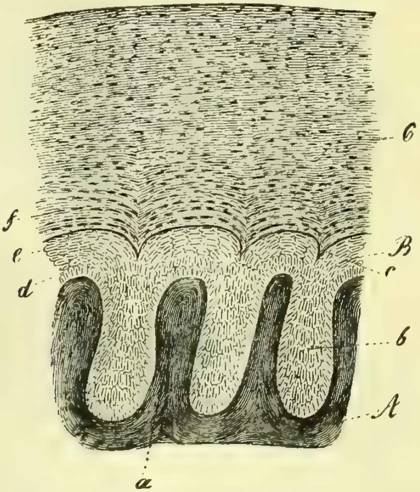

Fig. 237.—*Vertical transverse section through a small portion of the nail and matrix largely magnified.* *A*, corium of the nail-bed, raised into ridges or laminæ *a*, fitting in between corresponding laminæ *b*, of the nail. *B*, Malpighian, and *C*, horny layer of nail: *d*, deepest and vertical cells; *e*, upper flattened cells of Malpighian layer (Kölliker).

Functions of the Skin.

(1.) By means of its toughness, flexibility and elasticity, the skin is eminently qualified to serve as the general integument of the body, for defending the internal parts from external violence, and readily yielding and adapting itself to their various movements and changes of position.

(2.) The skin is the chief organ of the sense of touch. Its whole surface is extremely sensitive; but its *tactile* properties are due more especially to the abundant papillæ with which it is studded. (See Chapter on Special Senses.)

Although destined especially for the sense of touch, the papillæ are not so placed as to come into direct contact with external objects; but like the rest of the surface of the skin, are covered by one or more layers of epithelium, forming the cuticle or epidermis. The papillæ adhere very intimately to the cuticle, which is thickest in the spaces between them, but tolerably level on its outer surface: hence, when stripped off from the cutis, as after maceration, its internal surface presents a series of pits and elevations corresponding to the papillæ and their interspaces, of which it thus forms a kind of mould. Besides affording by its impermeability a check to undue evaporation from the skin, and providing the sensitive cutis with a protecting investment, the cuticle is of service in relation to the sense of touch. For by being thickest in the spaces, between the papillæ, and only thinly spread over the summits of these processes, it may serve to subdivide the sentient surface of the skin into a number of isolated points, each of which is capable of receiving a distinct impression from an external body. By covering the papillæ it renders the sensation produced by external bodies more obtuse, and in this manner also is subservient to touch: for unless the very sensitive papillæ were thus defended, the contact of substances would give rise to pain, instead of the ordinary impressions of touch. This is shown in the extreme sensitiveness and loss of tactile power in a part of the skin when deprived of its epidermis. If the cuticle is very thick, however, as on the heel, touch becomes imperfect, or is lost.

(3.) **The Secretion of Sebaceous Glands, and Hair-follicles.**—The secretion of the *sebaceous* glands and *hair-follicles* (for their products cannot be separated) consists of cast-off epithelium-cells, with nuclei and granules, together with an oily matter, extractive matter, and stearin; in certain parts, also, it is mixed with a peculiar odorous principle, which contains caproic, butyric, and rutic acids. It is, perhaps, nearly similar in composition to the unctuous coating, or *vernix caseosa*, which is formed on the body of the fœtus while in the uterus, and which contains large quantities of ordinary fat. Its purpose seems to be that of keeping the skin moist and supple and, by its oily nature, of both hindering the evaporation from the surface, and guarding the skin from the effects of the long-continued action of moisture. But while it thus serves local purposes, its removal from the body entitles it to be reckoned among the excretions of the skin; though the share it has in the purifying of the blood cannot be discerned.

(4.) **The Excretion of the Skin: the Sweat.**—The fluid secreted by the *sudoriferous* glands is usually formed so gradually, that the watery portion of it escapes by evaporation as fast as it reaches the surface. But, during strong exercise, exposure to great external warmth, in some diseases, and when evaporation is prevented, the secretion becomes more sensible, and collects on the skin in the form of drops of fluid.

The *perspiration* of the skin, as the term is sometimes employed in physiology, includes all that portion of the secretions and exudations from the skin which passes off by evaporation; the *sweat* includes that which may be collected only in drops of fluid on the surface of the skin. The two terms are, however, most often used synonymously; and for distinction, the former is called *insensible* perspiration; the latter *sensible* perspiration. The fluids are the same, except that the sweat is commonly mingled with various substances lying on the surface of the skin. The contents of the sweat are, in part, matters capable of assuming the form of vapour, such as carbonic acid and water, and in part, other matters which are deposited on the skin, and mixed with the sebaceous secretion.

TABLE OF THE CHEMICAL COMPOSITION OF SWEAT.

Water		995
Solids:—		
Organic Acids (formic, acetic, butyric, propionic, caproic, caprylic)	·9	
Salts, chiefly sodium chloride	1·8	
Neutral fats and cholesterin	·7	
Extractives (including urea), with epithelium	1·6	5
		1000

Of these several substances, however, only the carbonic acid and water need particular consideration.

Watery vapour.—The quantity of *watery vapour* excreted from the skin is on an average between $1\frac{1}{2}$ and 2 lb. daily. This subject has been estimated very carefully by Lavoisier and Sequin. The latter chemist enclosed his body in an air-tight bag, with a mouth-piece. The bag being closed by a strong band above, and the mouth-piece adjusted and gummed to the skin around the mouth, he was weighed, and then remained quiet for several hours, after which time he was again weighed. The difference in the two weights indicated the amount of loss by pulmonary exhalation. Having taken off the air-tight dress, he was immediately weighed again, and a fourth time after a certain interval. The difference between the two weights last ascertained gave the amount of the cutaneous and pulmonary exhalation together; by subtracting from this the loss by pulmonary exhalation alone, while he was in the air-tight dress, he ascertained the amount of cutaneous transpiration. During a state of rest, the average loss by cutaneous and pulmonary exhalation in a minute, is eighteen grains,—the minimum eleven grains, the maximum thirty-two grains; and of the eighteen grains, eleven pass off by the skin, and seven by the lungs.

The quantity of watery vapour lost by transpiration is of course influenced by all external circumstances which affect the exhalation from other evaporating surfaces, such as the temperature, the hygrometric state, and the stillness of the atmosphere. But, of the variations to which it is subject under the influence of these conditions, no calculation has been exactly made.

Carbonic Acid.—The quantity of *carbonic acid* exhaled by the skin on an average is about $\frac{1}{150}$ to $\frac{1}{200}$ of that furnished by the pulmonary respiration.

The cutaneous exhalation is most abundant in the lower classes of animals, more particularly the naked Amphibia, as frogs and toads, whose skin is thin and moist, and readily permits an interchange of gases between the blood circulating in it and the surrounding atmosphere. Bischoff found that, after the lungs of frogs had been tied and cut out, about a quarter of a cubic inch of carbonic acid gas was exhaled by the skin in eight hours. And this quantity is very large, when it is remembered that a full-sized frog will generate only about half a cubic inch of carbonic acid by his lungs and skin together in six hours. (Milne-Edwards and Müller.)

The importance of the respiratory function of the skin, which was once thought to be proved by the speedy death of animals whose skins, after removal of the hair, were covered with an impermeable varnish, has been shown by further observations to have no foundation in fact; the immediate cause of death in such cases being the loss of temperature. A varnished animal is said to have suffered no harm when surrounded by cotton wadding, and to have died when the wadding was removed.

Influence of the Nervous System on Excretion.—Any increase in the amount of sweat secreted is usually accompanied by dilatation of the cutaneous vessels. It is, however, probable that the secretion is like the other secretions, *e.g.*, the saliva, under the direct action of a special nervous apparatus, in that various nerves contain fibres which act directly upon the cells of the sweat glands in the same way that the chorda tympani contains fibres which act directly upon the salivary cells. The nerve fibres which induce sweating may act independently of the vaso-motor fibres, whether vaso-dilator or vaso-constrictor. The local apparatus is under control of the central nervous system—sweat centres probably existing both in the medulla and spinal cord—and may be reflexly as well as directly excited. This will explain the fact that sweat occurs not only when the skin is red, but also when it is pale, and the cutaneous circulation languid, as in the sweat which accompanies syncope or fainting, or which immediately precedes death.

(5.) **Absorption by the Skin.**—Absorption by the skin has been already mentioned, as an instance in which that process is most actively accomplished. Metallic preparations rubbed into the skin have the same action as when given internally, only in a less degree. Mercury applied in this manner exerts its specific influence upon syphilis, and excites salivation; potassio-tartrate of antimony may excite vomiting, or an eruption extending over the whole body; and arsenic may produce poisonous effects. Vegetable matters, also, if soluble, or already in solution, give rise to their peculiar effects, as cathartics, narcotics, and the like, when rubbed into the skin. The effect of rubbing is probably to convey the particles of the matter into the orifices of the glands whence they are more readily absorbed than they would be through the epidermis. When simply left in contact with the skin, substances, unless in a fluid state, are seldom absorbed.

It has long been a contested question whether the skin covered with the epidermis has the power of absorbing water; and it is a point the more difficult to determine because the skin loses water by evaporation. But, from the result of many experiments, it may now be regarded as a well-ascertained fact that such absorption really occurs. The absorption of water by the surface of the body may take place in the lower animals very rapidly. Not only frogs, which have a thin skin, but lizards, in which the cuticle is thicker than in man, after having lost weight by being kept for some time in a dry atmosphere, were found to recover both their weight and plumpness very rapidly when immersed in water. When merely the tail, posterior extremities, and posterior part of the body of the lizard were immersed, the water absorbed was distributed throughout the system. And a like absorption through the skin, though to a less extent, may take place also in man.

In severe cases of dysphagia, when not even fluids can be taken into the stomach, immersion in a bath of warm water or of milk and water may assuage the thirst; and it has been found in such cases that the weight of the body is increased by the immersion. Sailors also, when destitute of fresh water, find their urgent thirst allayed by soaking their clothes in salt water and wearing them in that state; but these effects are in part due to the hindrance to the evaporation of water from the skin.

(6.) **Regulation of Temperature.**—For an account of this important function of the skin, see Chapter on Animal Heat.

CHAPTER XIII.

THE KIDNEYS AND THE EXCRETION OF URINE.

The Kidneys are two in number, and are situated deeply in the lumbar region of the abdomen, on either side of the spinal column, behind the peritoneum. They correspond in position to the last two dorsal and two upper lumbar vertebræ; the right being slightly lower than the left in consequence of the position of the liver on the right side of the abdomen. They are characteristic in shape, about 4 inches long, 2½ inches broad, and 1½ inch thick. The weight of each kidney is about 4½ oz.

Structure of the Kidneys.—The kidney is covered by a rather tough fibrous capsule, which is slightly attached by its inner surface to the proper substance of the organ by means of very fine fibres of areolar tissue and minute blood-vessels. From the healthy kidney, therefore, it may be easily torn off without injury to the subjacent cortical portion of the organ. At the *hilus* or notch of the kidney, it becomes continuous with the external coat of the upper and dilated part of the ureter (fig. 238).

On making a section lengthwise through the kidney (fig. 238) the main part of its substance is seen to be composed of two chief portions, called respectively the *cortical* and the *medullary* portion, the latter being also sometimes called the *pyramidal* portion, from the fact of its being composed of about a dozen conical bundles of urine-tubes, each bundle being called a pyramid. The upper part of the duct of the organ, or the *ureter*, is dilated into what is called the *pelvis* of the kidney; and this, again, after separating into two or three principal divisions, is finally subdivided into still smaller portions, varying in number from about 8 to 12, or even more, and called *calyces.* Each of these little calyces or cups, which are often arranged in a double row, receives the pointed extremity or *papilla* of a *pyramid.* Sometimes, however, more than one papilla is received by a *calyx.*

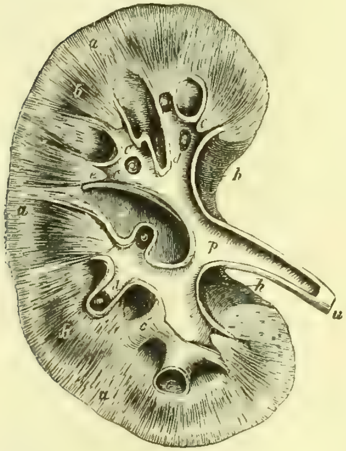

Fig. 238.—*Plan of a longitudinal section through the pelvis and substance of the right kidney,* $\frac{1}{2}$; *a*, the cortical substance; *b*, *b*, broad part of the pyramids of Malpighi; *c*, *c*, the divisions of the pelvis named calyces, laid open; *c'*, one of those unopened; *d*, summit of the pyramids of papillæ projecting into calyces; *e*, *e*, section of the narrow part of two pyramids near the calyces; *p*, pelvis or enlarged divisions of the ureter within the kidney; *u*, the ureter; *s*, the sinus; *h*, the hilus.

The kidney is a compound *tubular* gland, and both its cortical and medullary portions are composed essentially of secreting tubes, the *tubuli uriniferi*, which, by one extremity, in the *cortical* portion, end commonly in little saccules containing blood-vessel called *Malpighian bodies*, and, by the other, open through the *papillæ* into the pelvis of the kidney, and thus discharge the urine which flows through them.

In the pyramids the tubes are chiefly straight—dividing and diverging as they ascend through these into the cortical portion; while in the latter region they spread out more irregularly, and become much branched and convoluted.

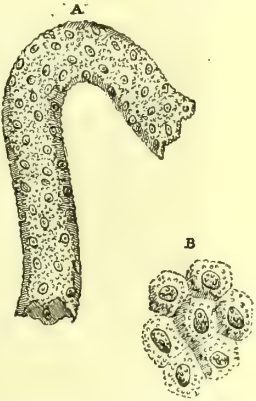

Fig. 239.—A. *Portion of a secreting tubule from the cortical substance of the kidney.* B. The epithelial or gland-cells. × 700 times.

Tubuli Uriniferi.—The tubuli uriniferi (fig. 239) are composed of a nearly homogeneous membrane, and are lined internally by epithelium. They vary considerably in size in different parts of their course, but are, on an average, about $\frac{1}{600}$ of an inch in diameter, and are found to be made up of several distinct sections which differ from one another very markedly, both in situation and structure. According to Klein, the following segments may be made out: (1) *The Malpighian corpuscle* (figs. 240, 241), composed of a hyaline membrana propria, thickened by a varying amount of fibrous tissue, and lined by flattened nucleated epithelial plates. This capsule is the dilated extremity of the uriniferous tubule, and contains within it a glomerulus of convoluted capillary blood-vessels supported by connective tissue, and covered by flattened epithelial plates. The glomerulus is connected with an efferent and an afferent vessel. (2) The constricted *neck* of the capsule (fig. 240, 2), lined in a similar manner, connects it with (3) The *Proximal convoluted tubule*, which forms several distinct curves and is lined with short columnar cells, which vary somewhat in size. The tube next passes almost vertically downwards, forming (4) The *Spiral tubule*, which is of much the same diameter, and is lined in the same way as the convoluted portion. So far the tube has been contained in the cortex of the kidney, it now passes vertically downward through the most external part (boundary layer) of the Malpighian pyramid into the more internal part (papillary layer), where it curves up sharply,

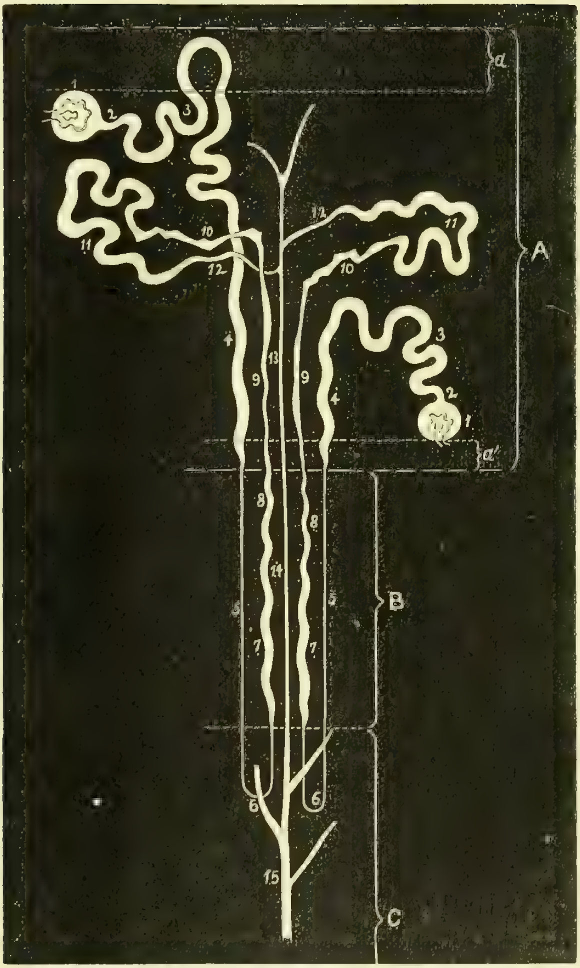

Fig. 240.—*A Diagram of the sections of uriniferous tubes.* A, Cortex limited externally by the capsule; *a*, subcapsular layer not containing Malpighian corpuscles; *a′* inner stratum of cortex, also without Malpighian capsules; B, Boundary layer; C, Papillary part next the boundary layer; 1, Bowman's capsule of Malpighian corpuscle; 2, neck of capsule; 3, proximal convoluted tubule; 4, spiral tubule of Schachowa; 5, descending limb of Henle's loop; 6, the loop proper; 7, thick part of the ascending limb; 8, spiral part of ascending limb; 9, narrow ascending limb in the medullary ray; 10, the irregular tubule; 11, the intercalated section of Schweigger-Seidel, or the distal convoluted tubule; 12, the curved collecting tubule; 13, the straight collecting tubule of the medullary ray; 14, the collecting tube of the boundary layer; 15, the large collecting tube of the papillary part which, joining with similar tubes, forms the duct. (Klein and Noble Smith.)

forming altogether the (5 and 6) *Loop of Henle*, which is a very narrow tube lined with flattened nucleated cells. Passing vertically upwards just as the tube reaches the boundary layer (7) it suddenly enlarges and becomes lined with polyhedral cells. (8) About midway in the boundary layer the tube again narrows, forming the *ascending spiral of Henle's loop*, but is still lined with polyhedral cells. At the point where the tube enters the cortex, (9) the ascending limb narrows, but the diameter varies considerably; here and there the cells are more flattened, but both in this as in (8), the cells are in many places very angular, branched, and imbricated. It then joins (10) the "*irregular tubule*," which has a very irregular and angular outline, and is lined with angular and imbricated cells. The tube next becomes convoluted, (11) forming the *distal convoluted tube or intercalated section of Schweigger*

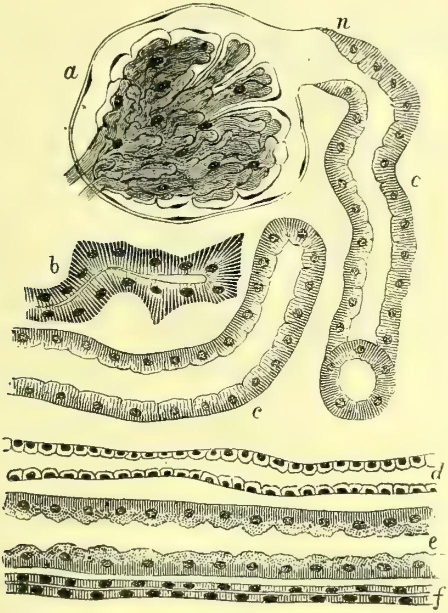

Fig. 241.—*From a vertical section through the kidney of a dog*—the capsule of which is supposed to be on the right. *a*. The capillaries of the Malpighian corpuscle—viz., the glomerulus, are arranged in lobules; *n*, neck of capsule; *c*, convoluted tubes cut in various directions; *b*, irregular tubule; *d*, *e*, and *f*, are straight tubes running towards capsules forming a so-called *medullary ray*; *d*, collecting tube; *e*, spiral tube; *f*, narrow section of ascending limb. × 380. (Klein and Noble Smith.)

Seidel, which is identical in all respects with the proximal convoluted tube (12 and 13). The curved and straight collecting tubes, the former entering the latter at right angles, and the latter passing vertically downwards, are lined with polyhedral, or spindle-shaped, or flattened, or angular cells. The straight collecting tube now enters the boundary layer (14), and passes on to the papillary layer, and, joining with other collecting tubes, form larger tubes, which finally open at the apex of the papilla. These collecting tubes are lined with transparent nucleated columnar or cubical cells (14, 15, 16).

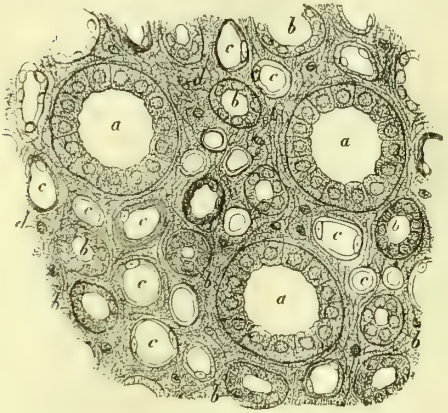

Fig. 242.—*Transverse section of a renal papilla*; *a*, larger tubes or papillary ducts; *b*, smaller tubes of Henle; *c*, blood-vessels, distinguished by their flatter epithelium; *d*, nuclei of the stroma (Kölliker). × 300.

The cells of the tubules with the exception of Henle's loop and all parts of the collecting tubules, are, as a rule, possessed of the intranuclear as well as of the intra-cellular network of fibres, of which the vertical rods are most conspicuous parts.

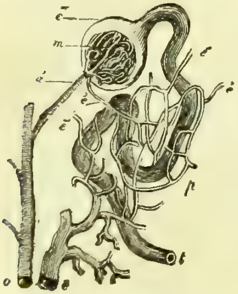

Fig. 243.—*Diagram showing the relation of the Malpighian body to the uriniferous ducts and blood-vessels.* *a*, one of the interlobular arteries; *a'*, afferent artery passing into the glomerulus; *c*, capsule of the Malpighian body, forming the termination of and continuous with *t*, the uriniferous tube; *e'*, *e'*, efferent vessels which subdivide in the plexus *p*, surrounding the tube, and finally terminate in the branch of the renal vein *e* (after Bowman).

Heidenhain observed that indigo-sulphate of sodium, and other pigments injected into the jugular vein of an animal, were apparently excreted by the cells which possessed these rods, and therefore concluded that the pigment passes through the cells, rods, and nucleus themselves. Klein, however believes that the pigment passes through the intercellular substances, and not through the cells.

In some places, it is stated that a distinct membrane of flattened cells can be made out lining the lumen of the tubes (*centrotubular membrane*).

Blood-vessels of Kidney.—In connection with the general distribution of blood-vessels to the kidney, the *Malpighian Corpuscles* may be further considered. They (fig. 243) are found only in the cortical part of the kidney, and are confined to the central part, which, however, makes up about seven-eighths of the whole cortex. On a section of the organ, some of them are just visible to the naked eye as minute red points; others are too small to be thus seen. Their average diameter is about $\frac{1}{120}$ of an inch. Each of them is composed, as we have seen above, of the dilated extremity of an urinary tube, or Malpighian *capsule*, enclosing a tuft of blood-vessels.

The renal artery divides into several branches, which, passing in at the hilus of the kidney, and covered by a fine sheath of areolar tissue derived from the capsule, enter the substance of the organ in the intervals between the papillæ, chiefly at the junction between the cortex and the boundary layer. The chief branches then pass almost horizontally, giving off smaller branches upwards to the cortex and downwards to the medulla. The former are for the most part straight, they pass almost vertically to the surface of the kidney, giving off laterally in all directions longer or shorter branches, which supply the afferent arteries to the Malpighian bodies.

The small *afferent* artery (figs. 243 and 245) which enters the Malpighian corpuscle, breaks up as before mentioned in the interior into a dense and convoluted and looped capillary plexus, which is ultimately gathered up again into a single small *efferent* vessel, comparable to a minute vein, which leaves the Malpighian capsule just by the point at which the afferent artery enters it. On leaving, it does not immediately join other small veins as might have been expected, but again breaking up into a network of capillary vessels, is distributed on the exterior of the tubule, from whose dilated end it had just emerged. After this second breaking up it is finally collected into a small vein, which, by union with others like it, helps to form the radicles of the renal vein.

Thus, in the kidney, the blood entering by the renal artery traverses *two* sets of capillaries before emerging by the renal vein, an arrangement which may be compared to the *portal* system in miniature.

The tuft of vessels in the course of development is, as it were thrust into the dilated extremity of the urinary tubule, which finally completely invests it just as the pleura invests the lungs or the tunica vaginalis the testicle. Thus the Malpighian capsule is lined by a parietal layer of squamous cells and a visceral or reflected layer immediately covering the vascular tuft (fig. 241), and sometimes dipping down into its interstices. This reflected layer of epithelium is readily seen in young subjects, but cannot always be demonstrated in the adult. (See figs. 244 and 245.)

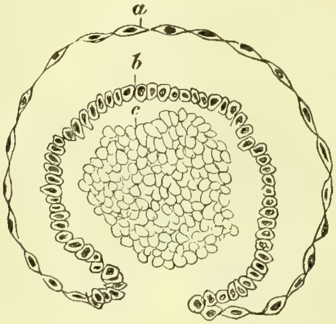

Fig. 244.—*Transverse section of a developing Malpighian capsule and tuft* (human) × 300. From a fœtus at about the fourth month; *a*, flattened cells growing to form the capsule; *b*, more rounded cells, continuous with the above, reflected round *c*, and, finally enveloping it; *c*, mass of embryonic cells which will later become developed into blood-vessels (W. Pye).

The vessels which enter the medullary layer break up into smaller arterioles, which pass through the boundary layer and proceed in a straight course between the tubules of the papillary layer, giving off on their way branches, which form a fine arterial meshwork around the tubes, and end in a similar plexus, from which the venous radicles arise.

Besides the small *afferent* arteries of the Malpighian bodies, there are, of course, others which are distributed in the ordinary manner, for nutrition's sake, to the different parts of the organ; and in the pyramids, between the tubes, there are numerous straight vessels, the *vasta recta*, supposed by some observers to be branches of *vasa efferentia* from Malpighian bodies, and therefore comparable to the venous plexus around the tubules in the *cortical* portion, while others think that they arise directly from small branches of the renal arteries.

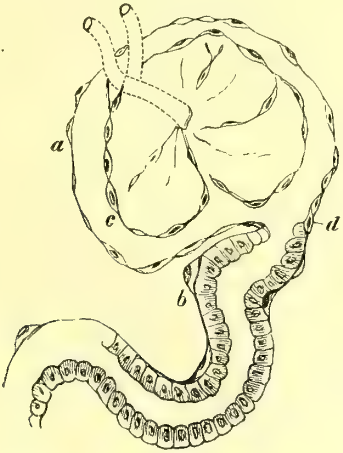

Fig. 245.—*Epithelial elements of a Malpighian capsule and tuft*, with the commencement of a urinary tubule showing the afferent and efferent vessel; *a*, layer of tesselated epithelium forming the capsule; *b*, similar, but rather larger epithelial cells, placed in the walls of the tube; *c*, cells, covering the vessels of the capillary tuft; *d*, commencement of the tubule, somewhat narrower than the rest of it (W. Pye).

Between the tubes, vessels, etc., which make up the substance of the kidney, there exists, in small quantity, a fine matrix of areolar tissue.

Nerves.—The nerves of the kidney are derived from the renal plexus.

Structure of the Ureters.—The duct of the kidney, or *ureter*, is a tube about the size of a goose-quill, and from a foot to sixteen inches in length, which, continuous above with the pelvis of the kidney, ends below by perforating obliquely the walls of the bladder, and opening on its internal surface. It is constructed of three principal coats (*a*) an outer, tough, *fibrous and elastic* coat; (*b*) a middle, *muscular coat*, of which the fibres are unstriped, and arranged in three layers—the fibres of the central layer being circular, and those of the other two longitudinal in direction; and (*c*) an internal *mucous* lining continuous with that of the pelvis of the kidney above, and of the urinary bladder below. The epithelium of all these parts (fig. 246) is alike stratified and of a somewhat peculiar form; the cells on the free surface of the mucous membrane being usually spheroidal or polyhedral with one or more spherical or oval nuclei; while beneath these are pear-shaped cells, of which the broad ends are directed towards the free surface, fitting in beneath the cells of the first row, and the apices are prolonged into processes of various lengths, among which, again, the deepest cells of the epithelium are found spheroidal, irregularly oval, spindle-shaped or conical.

Structure of Urinary Bladder.—The urinary bladder, which forms a receptacle for the temporary lodgment of the urine in the intervals of its expulsion from the body, is more or less pyriform, its widest part, which is situate above and behind, being termed the *fundus*: and the narrow constricted portion in front and below, by which it becomes continuous with the urethra, being called its *cervix* or *neck*. It is constructed of four principal coats, —*serous*, *muscular*, *areolar* or *submucous*, and *mucous*. (*a*) The *serous* coat, which covers only the posterior and upper half of the bladder, has the same structure as that of the peritoneum, with which it is continuous. (*b*) The fibres of the *muscular* coat, which are unstriped, are arranged in three principal layers, of which the external and internal (Ellis) have a general longitudinal, and the middle layer a circular direction. The latter are especially developed around the *cervix* of the organ, and are described as forming a *sphincter vesicæ*. The muscular fibres of the bladder, like those of the stomach, are arranged not in simple circles, but in figure-of-8 loops. (*c*) The *areolar* or *submucous* coat is constructed of connective tissue with a large proportion of elastic fibres. (*d*) The *mucous* membrane, which is rugose in the contracted state of the organ, does not differ in essential structure from mucous membranes in general. Its epithelium is stratified and closely resembles that of the pelvis of the kidney and the ureter (fig. 246).

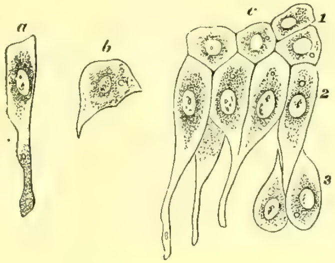

Fig. 246.—*Epithelium of the bladder*; *a*, one of the cells of the first row; *b*, a cell of the second row; *c*, cells *in situ*, of first, second, and deepest layers (Obersteiner).

The mucous membrane is provided with mucous glands, which are more numerous near the neck of the bladder.

The bladder is well provided with blood- and lymph-vessels, and with nerves. The latter are branches from the sacral plexus (spinal) and hypogastric plexus (sympathetic). A few ganglion-cells are found, here and there, in the course of the nerve-fibres.

The Excretion of the Kidney:—The Urine.

Physical Properties.—Healthy urine is a perfectly transparent, amber-coloured liquid, with a peculiar, but not disagreeable odour, a bitterish taste, and slight acid reaction. Its specific gravity varies from 1015 to 1025. On standing for a short time, a little mucus appears in it as a flocculent cloud.

Chemical Composition. — The urine consists of water, holding in solution certain organic and saline matters as its ordinary constituents, and occasionally various matters taken into the stomach as food—salts, colouring matter, and the like.

TABLE OF THE CHEMICAL COMPOSITION OF THE URINE (MODIFIED FROM BECQUEREL).

Water	967
Urea	14·230
Other nitrogenous crystalline bodies—	10·635
Uric acid, principally in the form of alkaline urates, a trace only free.	
Kreatinin, xanthin, hypoxanthin.	
Hippuric acid, leucin, tyrosin, taurin, cystin, &c., all in small amounts and not constant.	
Mucus and pigment.	
Salts :—	
Inorganic—	8·135
Principally sulphates, phosphates, and chlorides of sodium, and potassium, with phosphates of magnesium and calcium, traces of silicates and of chlorides.	
Organic—	
Lactates, hippurates, acetates and formates, which only appear occasionally.	
Sugar	a trace sometimes.
Gases (nitrogen and carbonic acid principally).	
	1000

Reaction of the Urine.—The normal reaction of the urine is slightly acid. This acidity is due to acid phosphate of sodium, and is less marked after meals. The urine contains no appreciable amount of free acid, as it gives no precipitate with sodium hyposulphite. After standing for some time the acidity increases from a kind of fermentation, due in all probability to the presence of mucus, and acid urates or free uric acid is deposited. After a time, varying in length according to the temperature, the reaction becomes strongly alkaline from the change of urea into ammonium carbonate—while at the same time a strong ammoniacal and fœtid odour appears, with deposits of triple phosphates and alkaline urates. As this does not occur unless the urine is exposed to the air, or, at least, until air has had access to it, it is probable that the decomposition is due to atmospheric germs.

Reaction of Urine in different classes of Animals.—In most herbivorous animals the urine is alkaline and turbid. The difference depends, not on any peculiarity in the mode of secretion, but on the differences in the food on which the two classes subsist: for when carnivorous animals, such as dogs, are restricted to a vegetable diet, their urine becomes pale, turbid, and alkaline, like that of an herbivorous animal, but resumes its former acidity on the return to an animal diet; while the urine voided by herbivorous animals, *e.g.*, rabbits, fed for some time exclusively upon animal substances, presents the acid reaction and other qualities of the urine of Carnivora, its ordinary alkalinity being restored only on the substitution of a vegetable for the animal diet. Human urine is not usually rendered alkaline by vegetable diet, but it becomes so after the free use of alkaline medicines, or of the alkaline salts with carbonic or vegetable acids; for these latter are changed into alkaline carbonates previous to elimination by the kidneys.

Average quantity of the chief constituents of the Urine excreted in 24 hours by healthy male adults (Parkes).

Water		52·	fluid ounces.
Urea		512·4	grains.
Uric acid		8·5	,,
Hippuric acid, uncertain		probably 10 to 15.	,,
Sulphuric acid		31·11	,,
Phosphoric acid		45·	,,
Potassium, Sodium, and Ammonium Chlorides and free Chlorine		323·25	,,
Lime		3·5	,,
Magnesia		3·	,,
Mucus		7·	,,
Extractives	Kreatinin Pigment Xanthin Hypoxanthin Resinous matter, &c.	154·	,,

Variations in Quantity of Constituents.—From these proportions, however, most of the constituents are, even in health, liable to variations. The variations of the water in different seasons, and according to the quantity of drink and exercise, have already been mentioned. The water of the urine is also liable to be influenced by the condition of the nervous system, being sometimes greatly increased in hysteria, and some other nervous affections; and at other times diminished. In some diseases it is enormously increased; and its increase may be either attended with an augmented quantity of solid matter, as in ordinary diabetes, or may be nearly the sole change, as in the affection termed diabetes insipidus. In other diseases, *e.g.*, the various forms of albuminuria, the quantity may be considerably diminished. A febrile condition almost always diminishes the quantity of water; and a like diminution is caused by any affection which draws off a large quantity of fluid from the body through any other channel than that of the kidneys, *e.g.*, the bowels or the skin.

Method of estimating the Solids.—A useful rule for approximately estimaling the total solids in any given specimen of healthy urine is to multiply the last two figures representing the specific gravity by 2·33. Thus, in urine of sp. gr. 1025, 2·33 × 25 = 58·25 grains of solids, are contained in 1000 grains of the urine. In using this method it must be remembered that the limits of error are much wider in diseased than in healthy urine.

Variations in the Specific Gravity.—The specific gravity of the human urine is about 1020. Probably no other animal fluid presents so many varieties in density within twenty-four hours as the urine does; for the relative quantity of water and of solid constituents of which it is composed is materially influenced by the condition and occupation of the body during the time at which it is secreted, by the length of time which has elapsed since the last meal, and by several other accidental circumstances. The existence of these causes of difference in the composition of the urine has led to the secretion being described under the three heads of *urina sanguinis*, *urina potus*, and *urina cibi*. The first of these names signifies the urine, or that part of it, which is secreted from the blood at times in which neither food nor drink has been recently taken, and is applied especially to the urine which is evacuated in the morning before breakfast. The terms *urina potus* indicates the urine secreted shortly after the introduction of any considerable quantity of fluid into the body: and the *urina cibi*, the portions secreted during the period immediately succeeding a meal of solid food. The last kind contains a larger quantity of solid matter than either of the others; the first or second, being largely diluted with water, possesses a comparatively low specific gravity. Of these three kinds, the morning urine is the best calculated for analysis in health, since it represents the simple secretion unmixed with the elements of food or drink; if it be not used, the whole of the urine passed during a period of twenty-four hours should be taken. In accordance with the various circumstances above-mentioned, the specific gravity of the urine may, consistently with health, range widely on both sides of the usual average. The average healthy range may be stated at from 1015 in the winter to 1025 in the summer; but variations of diet and exercise, and many other circumstances, may make even greater differences than these. In disease, the variation may be greater; sometimes descending, in albuminuria, to 1004, and frequently ascending in diabetes, when the urine is loaded with sugar, to 1050, or even to 1060.

Quantity.—The total quantity of urine passed in twenty-four hours is affected by numerous circumstances. On taking the mean of many observations by several experimenters, the average quantity voided in twenty-four hours by healthy male adults from 20 to 40 years of age has been found to amount to about 52½ fluid ounces (1½ to 2 litres).

Abnormal Constituents.—In disease, or after the ingestion of special foods, various abnormal substances occur in urine, of which the following may be mentioned—serum-albumin, globulin, ferments (apparently present in health also), blood, sugar, bile acids, and pigments, fats, oxalates, various salts taken as medicine, and other matters, as bacteria and renal casts.

The Solids of the Urine.

Urea.—(CH_4N_2O.)—Urea is the principal solid constituent of the urine, forming nearly one-half of the whole quantity of solid matter. It is also the most important ingredient, since it is the chief substance by which the nitrogen of decomposed tissue and superfluous food is excreted from the body. For its removal, the secretion of urine seems especially provided; and by its retention in the blood the most pernicious effects are produced.

Properties.—Urea, like the other solid constituents of the urine, exists in a state of solution. But it may be procured in the solid state, and then appears in the form of delicate silvery acicular crystals, which, under the microscope, appear as four-sided prisms (fig. 247). It is obtained in this state by evaporating urine carefully to the consistence of honey, acting on the inspissated mass with four parts of alcohol, then evaporating the alcoholic solution, and purifying the residue by repeated solution in water or alcohol, and finally allowing it to crystallize. It readily combines with some acids, like a weak base; and may thus be conveniently procured in the form of crystals of nitrate or oxalate of urea.

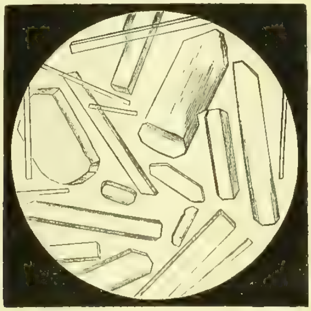

Fig. 247.—*Crystals of Urea.*

Urea is colourless when pure; when impure, yellow or brown: without smell, and of a cooling nitre-like taste; has neither an acid nor an alkaline re-action, and deliquesces in a moist and warm atmosphere. At 59° F. (15° C.) it requires for its solution less than its weight of water; it is dissolved in all proportions by boiling water; but it requires five times its weight of cold alcohol for its solution. It is insoluble in ether. At 248° F. (120° C.) it melts without undergoing decomposition; at a still higher temperature ebullition takes place, and carbonate of ammonium sublimes; the melting mass gradually acquires a pulpy consistence; and if the heat is carefully regulated, leaves a grey-white powder, cyanic acid.

Chemical Nature of Urea.—The chemical nature of urea is explained elsewhere,* but it will be as well to mention here that urea is isomeric with ammonium cyanate, and that it was first artificially produced from this substance. Thus:—Ammonium cyanate ($NH_4.\ CNO$) = urea (CH_4N_2O). The action of heat upon urea in evolving ammonium carbonate and leaving cyanic acid, is thus explained. A similar decomposition of the urea with development of ammonium carbonate ensues spontaneously when urine is kept for some days after being voided, and explains the ammoniacal odour then evolved (p. 438). The urea is sometimes decomposed before it leaves the bladder, when the mucous membrane is diseased, and the mucus secreted by it is both more abundant, and, probably, more prone to act as a ferment; although the decomposition does not often occur unless atmospheric germs have had access to the urine.

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* Appendix.

Variations in the Quantity of Urea.—The quantity of urea excreted is, like that of the urine itself, subject to considerable variation. For a healthy adult 500 grains (about 32·5 grms.) per diem may be taken as rather a high average. Its percentage in healthy urine is 1·5 to 2·5. It is materially influenced by diet, being greater when animal food is exclusively used, less when the diet is mixed, and least of all with a vegetable diet. As a rule, men excrete a larger quantity than women, and persons in the middle periods of life a larger quantity than infants or old people. The quantity of urea excreted by children, relatively to their body-weight, is much greater than in adults. Thus the quantity of urea excreted per kilogram of weight was, in a child, 0·8 grm.: in an adult only 0·4 grm. Regarded in this way, the excretion of carbonic acid gives similar results, the proportions in the child and adult being as 82 : 34.

The quantity of urea does not necessarily increase and decrease with that of the urine, though on the whole it would seem that whenever the amount of urine is much augmented, the quantity of urea also is usually increased; and it appears that the quantity of urea, as of urine, may be especially increased by drinking large quantities of water. In various diseases the quantity is reduced considerably below the healthy standard, while in other affections it is above it.

Estimation of Urea.—A convenient apparatus for estimating the quantity of urea in a given sample of urine is that devised by Russell and West.

Urea contains nearly half its weight of nitrogen; hence this gas may be taken as a measure of the urea. A small quantity of urine is mixed with a large excess of solution of sodium hypobromite, which completely decomposes the urea, liberating all the nitrogen in a gaseous form: a gentle heat promotes the reaction. The percentage of urea can of course be readily calculated from the volume of nitrogen evolved from a measured quantity of the urine, but this calculation is avoided by graduating the tube in which the nitrogen is collected with numbers which indicate the corresponding percentage of urea. $CON_2H_4 + 3NaBrO + 2NaHO = 3NaBr + 3H_2O + Na_2CO_3 + N_2$.

Uric Acid ($C_5H_4N_4O_3$).—This substance which was formerly termed lithic acid, on account of its existence in many forms of urinary calculi, is rarely absent from the urine of man or animals, though in the feline tribe it seems to be sometimes entirely replaced by urea. The proportionate quantity of uric acid varies considerably in different animals. In man, and Mammalia generally, especially the Herbivora, it is comparatively small. In the whole tribe of birds, and of serpents, on the other hand, the quantity is very large, greatly exceeding that of the urea. In the urine of granivorous birds, indeed, urea is rarely if ever found, its place being entirely supplied by uric acid.

Variations in Quantity.—The quantity of uric acid, like that of urea, in human urine, is increased by the use of animal food, and decreased by the use of food free from nitrogen, or by an exclusively vegetable diet. In most febrile diseases, and in plethora, it is formed in unnaturally large quantities; and in gout it is deposited in, and around, joints, in the form of urate of soda, of which the so-called chalk-stones of this disease are principally composed. The average amount secreted in twenty-four hours is 8·5 grains (rather more than half a gramme).

Condition of Uric Acid in the Urine.—The condition in which uric acid exists in solution in the urine has formed the subject of some discussion, because of its difficult solubility in water. It is found chiefly in the form of urate of sodium, produced by the uric acid as soon as it is formed combining with part of the base of the alkaline sodium phosphate of the blood. Hippuric acid, which exists in human urine also, acts upon the alkaline phosphate in the same way, and increases still more the quantity of acid phosphate, on the presence of which it is probable that a part of the natural acidity of the urine depends. It is scarcely possible to say whether the union of uric acid with the base sodium and probably ammonium, takes place in the blood, or in the act of secretion in the kidney: the latter is the more likely opinion; but the quantity of either uric acid or urates in the blood is probably too small to allow of this question being solved.

Owing to its existence in combination in healthy urine, uric acid for examination must generally be precipitated from its bases by a stronger acid. Frequently, however, when excreted in excess, it is deposited in a crystalline form (fig. 248), mixed with large quantities of ammonium or sodium urate. In such cases it may be procured for microscopic examination by gently warming the portion of urine containing the sediment; this dissolves urate of ammonium and sodium, while the comparatively insoluble crystals of uric acid subside to the bottom.

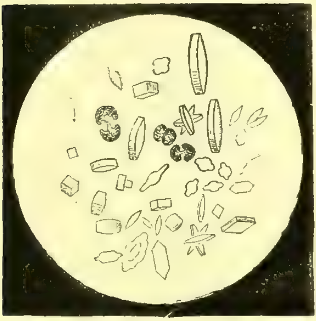

Fig. 248.—*Various forms of uric acid crystals.*

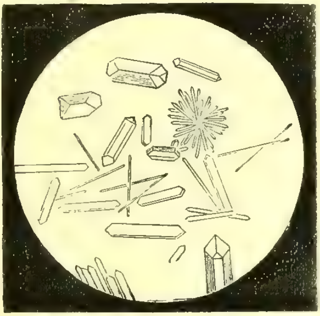

Fig. 249.—*Crystals of hippuric acid.*

The most common form in which uric acid is deposited in urine, is that of a brownish or yellowish powdery substance, consisting of granules of ammonium—or sodium urate. When deposited in crystals, it is most frequently in rhombic or diamond-shaped laminæ, but other forms are not uncommon (fig. 248). When deposited from urine, the crystals are generally more or less deeply coloured, from being combined with the colouring principles of the urine.

There are two chief tests for uric acid besides the microscopic evidence of its crystalline structure: (1) *The Murexide test*, which consists of evaporating to dryness a mixture of strong nitric acid and uric acid in a water bath. This leaves a yellowish-red residue of *Alloxan* ($C_4H_2N_2O_4$) and urea, and this, on addition of ammonium hydrate gives a beautiful purple (ammonium purpurate, C_8H_4 (NH_4) N_5O_6), deepened on addition of caustic potash. (2) *Schiff's test.* Dissolve the uric acid in sodium carbonate solution, and drop some of it on a filter paper moistened with silver nitrate, a black spot appears, which corresponds to the reduction of silver by the uric acid.

Hippuric Acid ($C_9H_9NO_3$) has long been known to exist in the urine of herbivorous animals in combination with soda. It also exists naturally in the urine of man, in quantity equal or rather exceeding that of the uric acid.

Pigments.—The colouring matters of the urine are: (1) *Uro-bilin*, a substance connected with the colouring matters of the blood and bile (p. 341); it is especially seen in febrile urine and exists normally, but to less amount; it is of a yellowish-red colour; (2) *Uro-chrome*, which on exposure undergoes oxydation, and becomes *Uro-erythrin*, the former being yellowish and the latter sandy red; and (3) *Indican* is occasionally present.

Indican is not itself pigmentary, though by its decomposition indigo blue and indigo red are produced. Its presence can usually be detected by adding to a small quantity of urine an equal bulk of strong hydrochloric acid, and gently heating the solution; on the addition of two or three drops of strong nitric acid a delicate purplish tint is developed, and indigo blue and red crystals separate out.

Mucus.—*Mucus* in the urine consists principally of the epithelial débris of the mucous surface of the urinary passages. Particles of epithelium, in greater or less abundance, may be detected in most samples of urine, especially if it has remained at rest for some time and the lower strata are then examined (fig. 250). As urine cools, the mucus is sometimes seen suspended in it as a delicate opaque cloud, but generally it falls. In inflammatory affections of the urinary passages, especially of the bladder, mucus

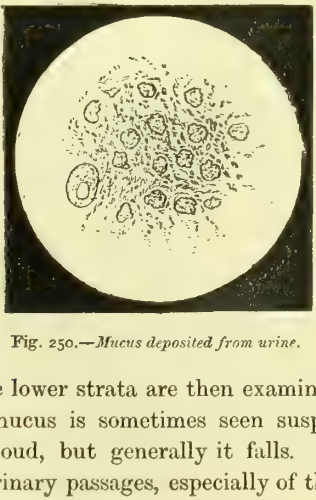

Fig. 250.—*Mucus deposited from urine.*

in large quantities is poured forth, and speedily undergoes decomposition. The presence of the decomposing mucus excites (as already stated, p. 438) chemical changes in the urea, whereby ammonia, or carbonate of ammonium, is formed, which, combining with the excess of acid in the super-phosphates in the urine, produces insoluble neutral or alkaline phosphates of calcium and magnesium, and phosphate of ammonium and magnesium. These mixing with the mucus, constitute the peculiar white, viscid, mortar-like substance which collects upon the mucous surface of the bladder, and is often passed with the urine, forming a thick tenacious sediment.

Extractives.—Besides mucus and colouring matter, urine contains a considerable quantity of nitrogenous compounds, usually described under the generic name of *extractives.* Of these, the chief are: (1) *Kreatinin* ($C_4H_7N_3O$) a substance derived, probably, from the metamorphosis of muscular tissue, crystallizing in colourless oblique rhombic prisms; a fairly definite amount of this substance, about 15 grains (1 grm.), appears in the urine daily, so that it must be looked upon as a normal constituent; it is increased on an increase of the nitrogenous constituents of the food; (2) *Xanthin* ($C_5N_4H_4O_2$), an amorphous powder soluble in hot water; (3) *Hypo-xanthin,* or sarkin ($C_5N_4H_4O$); (4) *Oxaluric acid* ($C_3H_4N_2O_4$), in combination with ammonium; (5) *Allantoin* ($C_4H_6N_4O_3$) in the urine of the new-born child. All these extractives are chiefly interesting as being closely connected with urea, and mostly yielding that substance on oxidation. Leucin and tyrosin can scarcely be looked upon as normal constituents of urine.

Saline Matter.—The *sulphuric acid* in the urine is combined chiefly or entirely with sodium or potassium; forming salts which are taken in very small quantity with the food, and are scarcely found in other fluids or tissues of the body; for the sulphates commonly enumerated among the constituents of the ashes of the tissues and fluids are for the most part, or entirely, produced by the changes that take place in the burning. Only about one-third of the sulphuric acid found in the urine is derived directly from the food (Parkes). Hence the greater part of the sulphuric acid which the sulphates in the urine contain, must be formed in the blood, or in the act of secretion of urine; the sulphur of which the acid is formed being probably derived from the decomposing nitrogenous tissues, the other elements of which are resolved into urea and uric acid. It may be in part derived also from the sulphur-holding *taurin* and *cystin*, which can be found in the liver, lungs, and other parts of the body, but not generally in the excretions; and which, therefore, must be broken up. The oxygen is supplied through the lungs, and the heat generated during combination with the sulphur, is one of the subordinate means by which the animal temperature is maintained.

Besides the sulphur in these salts, some also appears to be in the urine, uncombined with oxygen; for after all the sulphates have been removed from urine, sulphuric acid may be formed by drying and burning it with nitre. From three to five grains of sulphur are thus daily excreted. The combination in which it exists is uncertain: possibly it is in some compound analogous to cystin or cystic oxide (p. 449). Sulphuric acid also exists normally in the urine in combination with phenol (C_6H_6O) as phenol sulphuric acid or its corresponding salts, with sodium, &c.

The *phosphoric acid* in the urine is combined partly with the alkalies, partly with the alkaline earths—about four or five times as much with the former as with the latter. In blood, saliva, and other alkaline fluids of the body, phosphates exist in the form of alkaline, neutral, or acid salts. In the urine they are acid salts, viz., the sodium, ammonium, calcium, and magnesium phosphates, the excess of acid being (Liebig) due to the appropriation of the alkali with which the phosphoric acid in the blood is combined, by the several new acids which are formed or discharged at the kidneys, namely, the uric, hippuric, and sulphuric acids, all of which are neutralised with soda.

The phosphates are taken largely in both vegetable and animal food; some thus taken are excreted at once; others, after being transformed and incorporated with the tissues. Calcium phosphate forms the principal earthy constituent of bone, and from the decomposition of the osseous tissue the urine derives a large quantity of this salt. The decomposition of other tissues also, but especially of the brain and nerve-substance, furnishes large supplies of phosphorus to the urine, which phosphorus is supposed, like the sulphur, to be united with oxygen, and then combined with bases. This quantity is, however, liable to considerable variation. Any undue exercise of the brain, and all circumstances producing nervous exhaustion, increase it. The earthy phosphates are more abundant after meals, whether on animal or vegetable food, and are diminished after long fasting. The alkaline phosphates are increased after animal food, diminished after vegetable food. Exercise increases the alkaline, but not the earthy phosphates (Bence Jones). Phosphorus uncombined with oxygen appears, like sulphur, to be excreted in the urine (Ronalds). When the urine undergoes alkaline fermentation, phosphates are deposited in the form of an *urinary sediment*, consisting chiefly of ammonio-magnesium phosphate (triple phosphate) (fig. 251). This compound does not, as such, exist in healthy urine. The ammonia is chiefly or wholly derived from the decomposition of urea (p. 442).

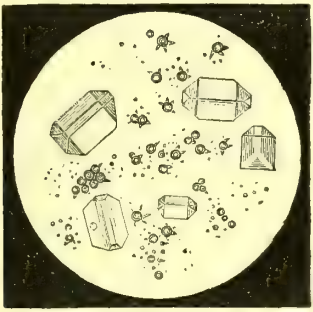

Fig. 251.—*Urinary sediment of triple phosphates* (large prismatic crystals) and urate of ammonium, from urine which had undergone alkaline fermentation.

The *chlorine* of the urine occurs chiefly in combination with sodium, but slightly also with ammonium, and, perhaps, potassium. As the chlorides exist largely in food, and in most of the animal fluids, their occurrence in the urine is easily understood.

Cystin ($C_3H_7N\,SO_2$) (fig. 252) is an occasional constituent of urine. It resembles taurin in containing a large quantity of sulphur—more than 25 per cent. It does not exist in healthy urine.

Another common morbid constituent of the urine is *oxalic acid*, which is frequently deposited in combination with calcium (fig. 253) as an urinary sediment. Like cystin, but much more commonly, it is the chief constituent of certain calculi.

Of the other abnormal constituents of the urine mentioned it will be unnecessary to speak at length in this work.

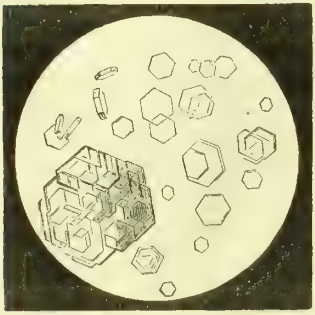

Fig. 252.—*Crystals of cystin.*

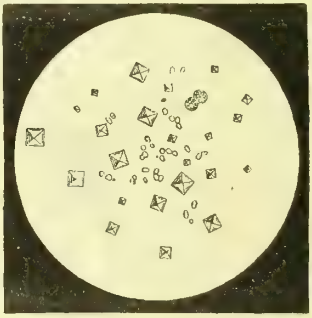

Fig. 253.—*Crystals of calcium oxalate.*

Gases.—A small quantity of gas is naturally present in the urine in a state of solution. It consists of carbonic acid (chiefly) and nitrogen and a small quantity of oxygen.

The Method of the Excretion of Urine.

The excretion of the urine by the kidney is believed to consist of two more or less distinct processes—viz., (1.) *of filtration*, by which the water and the ready-formed salts are eliminated; and, (2.) *of true secretion*, by which certain substances forming the chief and more important part of the urinary solids are removed from the blood. This division of function corresponds more or less to the division in the functions of other glands of which we have already treated. It will be as well to consider them separately.

(1.) **Of Filtration.**—This part of the renal function is performed within the Malpighian corpuscles by the renal glomeruli. By it not only the water is strained off, but also certain other constituents of the urine, *e.g.*, sodium chloride, are separated. The amount of the fluid filtered off depends almost entirely upon the blood-pressure in the glomeruli.

The greater the blood-pressure in the arterial system generally, and consequently in the renal arteries, the greater, *cæteris paribus*, will be the blood-pressure in the glomeruli, and the greater the quantity of urine separated; but even without increase of the general blood-pressure, if the renal arteries be locally dilated, the pressure in the glomeruli will be increased and with it the secretion of urine. On the other hand, if the local blood-pressure be diminished, the amount of fluid will be lessened. All the numerous causes, therefore, which increase the blood-pressure (p. 189) will, as a rule, secondarily increase the secretion of urine. Of these the heart's action is amongst the most important. When its contractions are increased in force, increased diuresis is the result. Similarly, causes which lower the blood-pressure, *e.g.*, enfeebled action of the heart, great loss of blood, &c., will diminish the activity of the secretion of urine.

The close connection between the blood-pressure generally and the nervous system has been before considered, and it will be clear, therefore, that the amount of urine secreted depends greatly upon the influence of the nervous system. Thus, division of the spinal cord, by producing general vascular dilatation, causes a great diminution of blood-pressure, and so diminishes the amount of water passed; since the local dilatation in the renal arteries is not sufficient to counteract the general diminution of pressure. Stimulation of the cut cord produces, strangely enough, the same results—*i.e.*, a diminution in the amount of the urine passed, but in a different way, viz., by constricting the arteries generally, and, among others, the renal arteries; the diminution of blood-pressure resulting from the local resistance in the renal arteries being more potent to diminish blood-pressure in the glomeruli than the general increase of blood-pressure is to increase it. Section of the renal nerves or of any others which produce *local* dilatation without greatly diminishing the general blood-pressure will cause an increase in the quantity of fluid passed.

The fact that in summer or in hot weather the urine is diminished may be attributed partly to the copious elimination of water by the skin in the form of sweat which occurs in summer, as contrasted with the greatly diminished functional activity of the skin in winter, but also to the dilated condition of the vessels of the skin causing a decrease in the general blood-pressure. Thus we see that in regard to the elimination of water from the system, the skin and kidneys perform similar functions, and are capable to some extent of acting vicariously, one for the other. Their relative activities are inversely proportional to each other.

The intimate connection between the condition of the kidney and the blood-pressure has been exceedingly well shown by the introduction of an instrument called the *Oncometer*, recently introduced by Roy, which is a modification of the plethysmograph (fig. 138). By means of this apparatus any alteration in the volume of the kidney is communicated to an apparatus (oncograph) capable of recording graphically, with a writing lever, such variations. It has been found that the kidney is extremely sensitive to any alteration in the general blood-pressure, every fall in the general blood-pressure being accompanied by a decrease in the volume of the kidney, and every rise, unless produced by considerable constriction of the peripheral vessels, including those of the kidney, being accompanied by a corresponding increase of volume. Increase of volume is followed by an increase in the amount of urine secreted, and decrease of volume by a decrease in the secretion. In addition, however, to the response of the kidney to alterations in the general blood-pressure, it has been further observed that certain substances, when injected into the blood, will also produce an increase in volume of the kidney, and consequent increased flow of urine, without affecting the general blood-pressure—such bodies as sodium acetate and other diuretics. These observations appear to prove that local dilatation of the renal vessels may be produced by alterations in the blood upon a local nervous mechanism, as the effect is produced when all of the renal nerves have been divided. The alterations are not only produced by the addition of drugs, but also by the introduction of comparatively small quantities of water or saline solution. To this alteration of the blood acting upon the renal vessels (either directly or) through a local vaso-motor mechanism, and not to any great alteration in the general blood-pressure, must we attribute the effect of meals, &c., observed by Roberts. "The renal excretion is increased after meals and diminished during fasting and sleep. The increase began within the first hour after breakfast, and continued during the succeeding two or three hours; then a diminution set in, and continued until an hour or two after dinner. The effect of dinner did not appear until two or three hours after the meal; and it reached its maximum about the fourth hour. From this period the excretion steadily decreased until bed-time. During sleep it sank still lower, and reached its minimum—being not more than one-third of the quantity excreted during the hours of digestion." The increased amount of urine passed after drinking large quantities of fluid probably depends upon the diluted condition of the blood thereby induced.

The following table * will help to explain the dependence of the filtration function upon the blood-pressure and the nervous system :—

TABLE OF THE RELATION OF THE SECRETION OF URINE TO ARTERIAL PRESSURE.

A. Secretion of urine may be increased—

- *a. By increasing the general blood-pressure*, by
    - 1. Increase of force or frequency of heart-beat.
    - 2. Constriction of small arteries of areas other than the kidney.
- *b. By relaxation of the renal artery without compensating relaxation elsewhere*, by
    - 1. Division of the renal nerves (causing polyuria).
    - 2. " " " and afterwards stimulating cord below medulla (causing greater polyuria).
    - 3. Division of the splanchnic nerves ; but polyuria is less than in 1 or 2, as these nerves are distributed to a wider area the dilatation of the renal artery is accompanied by dilatation of other vessels, and therefore with a somewhat diminished general blood supply.
    - 4. Puncture of the floor of fourth ventricle or mechanical irritation of the superior cervical ganglion of the sympathetic, possibly from dilatation of the renal arteries.

B. Secretion of urine may be diminished—

- *a. By diminishing the general blood-pressure*, by
    - 1. Diminishing the force or frequency of the heart-beats.
    - 2. Dilatation of capillary areas other than the kidney.
    - 3. Division of spinal cord below medulla, which causes dilatation of general abdominal area, and urine generally ceases being secreted.
- *b. By increasing the blood-pressure*, by stimulation of spinal cord below medulla, the constriction of the renal artery not being compensated for by the increase of general blood-pressure.
- *c. By constriction of the renal artery*, by stimulating the renal or splanchnic nerves, or by stimulating the spinal cord.

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* Modified from M. Foster.

Although it is convenient to call the processes which go on in the renal glomeruli, filtration, there is reason to believe that they are not absolutely mechanical, as the term might seem to imply, since, when the epithelium of the Malpighian capsule has been, as it were, put out of order by ligature of the renal artery, on removal of the ligature, the urine has been found temporarily to contain albumen, indicating that a selective power resides in the healthy epithelium, which allows a certain constituent part of the blood to be filtered off and not others.

(2.) **Of True Secretion.**—That there is a second part in the process of the excretion of urine, which is true secretion, is suggested by the structure of the tubuli uriniferi, and the idea is supported by various experiments. It will be remembered that the convoluted portions of the tubules are lined with epithelium, which bears a close resemblance to the secretory epithelium of other glands, whereas the Malpighian capsules and portions of the loops of Henle are lined simply by endothelium. The two functions are, then, suggested by the differences of epithelium, and also by the fact that the blood supply is different, since the convoluted tubes are surrounded by capillary vessels derived from the breaking up of the efferent vessels of the Malpighian tufts. The theory first suggested by Bowman (1842), and still generally accepted, of the function of the two parts of the tubules, is that the cells of the convoluted tubes, by a process of true secretion, separate from the blood substances such as urea, whereas from the glomeruli are separated the water and the inorganic salts. Another theory suggested by Ludwig (1844) is that in the glomeruli is filtered off from the blood all the constituents of the urine in a very diluted condition. When this passes along the tortuous uriniferous tube, part of the water is re-absorbed into the vessels surrounding them, leaving the urine in a more concentrated condition—retaining all its proper constituents. This osmosis is promoted by the high specific gravity of the blood in the capillaries surrounding the convoluted tubes, but the return of the urea and similar substances is prevented by the secretory epithelium of the tubules. Ludwig's theory, however plausible, must, we think, give way to the first theory, which is more strongly supported by direct experiment.

By using the kidney of the newt, which has two distinct vascular supplies, one from the renal artery to the glomeruli, and the other from the renal portal vein to the convoluted tubes, Nussbaum has shown that certain substances, *e.g.*, peptones, sugar, when injected into the blood, are eliminated by the glomeruli, and so are not got rid of when the renal arteries are tied; whereas certain other substances, *e.g.*, urea, when injected into the blood, are eliminated by the convoluted tubes, even when the renal arteries have been tied. This evidence is very direct that urea is excreted by the convoluted tubes.

Heidenhain also has shown by experiment that if a substance (sodium sulphindigotate), which ordinarily produces blue urine, be injected into the blood after section of the medulla which causes lowering of the blood-pressure in the renal glomeruli, that when the kidney is examined, the cells of the convoluted tubules (and of these alone) are stained with the substance, which is also found in the lumen of the tubules. This appears to show that under ordinary circumstances the pigment at any rate is eliminated by the cells of the convoluted tubules, and that when by diminishing the blood-pressure, the filtration of urine ceases, the pigment remains in the convoluted tubes, and is not, as it is under ordinary circumstances, swept away from them by the flushing of them which ordinarily takes place with the watery part of urine derived from the glomeruli. It therefore is probable that the cells, if they excrete the pigment, excrete urea and other substances also. But urea acts somewhat differently to the pigment, as when it is injected into the blood of an animal in which the medulla has been divided and the secretion of urine stopped, a copious secretion of urine results, which is not the case when the pigment is used instead under similar conditions. The flow of urine, independent of the general blood-pressure, might be supposed to be due to the action of the altered blood upon some local vaso-motor mechanism; and, indeed, the local blood-pressure is directly affected in this way, but there is reason for believing that part of the increase of the secretion is due to the direct stimulation of the cells by the urea contained in the blood.

To sum up, then, the relation of the two functions: (I.) The process of filtration, by which the chief part if not the whole of the *fluid* is eliminated, together with certain inorganic salts, and possibly other solids, is directly dependent upon blood-pressure, is accomplished by the renal glomeruli, and is accompanied by a free discharge of solids from the tubules. (2.) The process of secretion proper, by which urea and the principal urinary solids are eliminated, is only indirectly, if at all, dependent upon blood-pressure and is accomplished by the cells of the convoluted tubes. It is sometimes accompanied by the elimination of copious fluid, produced by the chemical stimulation of the epithelium of the same tubules.

Sources of the Nitrogenous Urinary Solids.

Urea.—In speaking of the method of the secretion of urine, it was assumed that the part played by the cells of the uriniferous tubules was that of mere separation of the constituents of the urine which existed ready-formed in the blood : there is considerable evidence to favour this assumption. What may be called the specially characteristic solid of the urine, *i.e.*, urea (as well as most of the other solids), may be detected in the blood, and in other parts of the body, *e.g.*, the humours of the eye (Millon), even while the functions of the kidneys are unimpaired : but when from any cause, especially extensive disease or extirpation of the kidneys, the separation of urine is imperfect, the urea is found largely in the blood and in most other fluids of the body.

It must, therefore, be clear that the urea is for the most part made somewhere else than in the kidneys, and simply brought to them by the blood for elimination. It is not absolutely proved, however, that all the urea is formed away from these organs, and it is possible that a small quantity is actually secreted by the cells of the tubules. The sources of the urea, which is brought to the kidneys for excretion, are stated to be two.

(1.) *From the splitting up the Elements of the Nitrogenous Food.*—The origin of urea from this source is shown by the increase which ensues on substituting an animal or highly nitrogenous for a vegetable diet ; in the much larger amount—nearly double—excreted by Carnivora than Herbivora, independent of exercise ; and in its diminution to about one-half during starvation, or during the exclusion of non-nitrogenous principles of food. Part, at any rate, of the increased amount of urea which appears in the urine soon after a full meal of proteid material may be attributed to the production of a considerable amount of leucin and tyrosin as by-products of pancreatic digestion. These substances are carried by the portal vein to the liver, and it is there that the change in all probability takes place; as when the functions of the organ are gravely interfered with, as in the case of acute yellow atrophy, the amount of urea is distinctly diminished, and its place appears to be taken by leucin and tyrosin. It has been found by experiment, too, that if these substances be introduced into the alimentary canal, the introduction is followed by a corresponding increase in the amount of urea, but not by the presence of the bodies themselves in the urine.

(2.) *From the nitrogenous metabolism of the tissues.*—This second origin of urea is shown by the fact that it continues to be excreted, though in smaller quantity than usual, when all nitrogenous substances are strictly excluded from the food, as when the diet consists for several days of sugar, starch, gum, oil, and similar non-nitrogenous substances (Lehmann). It is excreted also, even though no food at all be taken for a considerable time; thus it is found in the urine of reptiles which have fasted for months; and in the urine of a madman, who had fasted eighteen days, Lassaigne found both urea and all the components of healthy urine.

Turning to the muscles, however, as the most actively metabolic tissue, we find as a result of their activity not urea, but *kreatin;* and although it may be supposed that some of this latter body appears naturally in the urine as *kreatinin,* yet it is not in sufficient quantity to represent the large amount of it formed by the muscles, and, indeed, by others of the tissues. It is assumed that kreatin therefore is the nitrogenous antecedent of urea; where its conversion into urea takes place is doubtful, but very likely the liver, and possibly the spleen, may be the seats of the change. It may be, however, that part—but if so, a small part—reaches the kidneys without previous change, leaving it to the cells of the renal tubules to complete the action. In speaking of kreatin as the antecedent of urea, it should be recollected that other nitrogenous products, such as xanthin ($C_5 H_4 N_4 O_2$), appear in conjunction with it, and that these may also be converted into urea.

It was formerly taken for granted that the quantity of urea in the urine is greatly increased by *active exercise;* but numerous observers have failed to detect more than a slight increase under such circumstances; and our notions concerning the relation of this excretory product to the destruction of muscular fibre, consequent on the exercise of the latter, have undergone considerable modification. There is no doubt, of course, that like all parts of the body, the muscles have but a limited term of existence, and are being constantly although very slowly renewed, at the same time that a part of the products of their disintegration appears in the urine in the form of urea. But the waste is not so fast as it was formerly supposed to be; and the theory that the amount of work done by the muscle is expressed by the quantity of urea excreted in the urine must without doubt be given up.

Uric Acid.—Uric acid probably arises much in the same way as urea, either from the disintegration of albuminous tissues, or from the food. The relation which uric acid and urea bear to each other is, however, still obscure: but uric acid is said to be a less advanced stage of the oxidation of the products of proteid metabolism. The fact that they often exist together in the same urine, makes it seem probable that they have different origins; but the entire replacement of either by the other, as of urea by uric acid in the urine of birds, serpents, and many insects, and of uric acid by urea, in the urine of the feline tribe of Mammalia, shows that either alone may take the place of the two. At any rate, although it is true that one molecule of uric acid is capable of splitting up into two molecules of urea and one of mes-oxalic acid, there is no evidence for believing that uric acid is an antecedent of urea in the nitrogenous metabolism of the body. Some experiments seem to show that uric acid is formed in the kidney.

Hippuric Acid ($C_9H_9NO_3$)—Hippuric acid is closely allied to benzoic acid; and this substance when introduced into the system, is excreted by the kidneys as hippuric acid (Ure). Its source is not satisfactorily determined: in part it is probably derived from some constituents of vegetable diet, though man has no hippuric acid in his food, nor, commonly, any benzoic acid that might be converted into it; in part from the natural disintegration of tissues, independent of vegetable food, for Weismann constantly found an appreciable quantity, even when living on an exclusively animal diet. Hippuric acid arises from the union of benzoic acid with glycin ($C_2H_5NO_2 + C_7H_6O_2 = C_9H_9NO_3 + H_2O$), which union may take place in the kidneys themselves, as well as in the liver.

Extractives.—The source of the extractives of the urine is probably in chief part the disintegration of the nitrogenous tissues, but we are unable to say whether these nitrogenous bodies are merely accidental, having resisted further decomposition into urea, or whether they are the representatives of the decomposition of special tissues, or of special forms of metabolism of the tissues. There is, however, one exception, and this is in the case of kreatinin; there is great reason for believing that the amount of this body which appears in the urine is derived from the metabolism of the nitrogenous food, as when this is diminished, it diminishes, and when stopped, it no longer appears in the urine.

The Passage of Urine into the Bladder.

As each portion of urine is secreted it propels that which is already in the tubes onwards into the pelvis of the kidney. Thence through the ureter the urine passes into the bladder, into which its rate and mode of entrance has been watched in cases of *ectopia vesicæ*, *i.e.*, of such fissures in the anterior or lower part of the walls of the abdomen, and of the front wall of the bladder, as expose to view its hinder wall together with the orifices of the ureters. The urine does not enter the bladder at any regular rate, nor is there a synchronism in its movement through the two ureters. During fasting, two or three drops enter the bladder every minute, each drop as it enters first raising up the little papilla on which, in these cases the ureter opens, and then passing slowly through its orifice, which at once again closes like a sphincter. In the recumbent posture, the urine collects for a little time in the ureters, then flows gently, and, if the body be raised, runs from them in a stream till they are empty. Its flow is increased in deep inspiration, or straining, and in active exercise, and in fifteen or twenty minutes after a meal (Erichsen). The urine collecting is prevented from regurgitation into the ureters by the mode in which these pass through the walls of the bladder, namely, by their lying for between half and three-quarters of an inch between the muscular and mucous coats before they turn rather abruptly forwards, and open through the latter into the interior of the bladder.

Micturition.—The contraction of the muscular walls of the bladder may by itself expel the urine with little or no help from other muscles, when the sphincter of the organ is relaxed. In so far, however, as it is a *voluntary* act, micturition is performed by means of the abdominal and other expiratory muscles which, in their contraction, press on the abdominal viscera, the diaphragm being fixed, and cause the expulsion of the contents of the bladder. The muscular coat of the bladder co-operates, in micturition, by reflex *involuntary* action, with the abdominal muscles; and the act is completed by the *accelerator urinæ* which, as its name implies, quickens the stream, and expels the last drops of urine from the urethra. The act, so far as it is not directed by volition, is under the control of a nervous *centre* in the lumbar spinal cord, through which, as in the case of the similar centre for defæcation (p. 357), the various muscles concerned are harmonized in their action. It is well known that the act may be reflexly induced, *e.g.*, in children who suffer from intestinal worms, or other such irritation. Generally the afferent impulse which calls into action the desire to micturate is excited by over distention of the bladder, or even by a few drops of urine passing into the urethra.

CHAPTER XIV.

THE VASCULAR GLANDS.

The materials separated from the blood by the ordinary process of secretion in glands, are always discharged from the organ in which they are formed, and are either straightway expelled from the body, or if they are again received into the blood, it is only after they have been altered from their original condition, as in the cases of the saliva and bile. There appears, however, to be a modification of the process of secretion, in which certain materials are abstracted from the blood, undergo some change, and are added to the lymph or restored to the blood, without being previously discharged from the secreting organ, or made use of for any secondary purpose. The bodies in which this modified form of secretion takes place, are usually described as vascular glands, or glands without ducts, and include the *spleen*, the *thymus* and *thyroid* glands, the *supra-renal capsules*, the *pineal* gland and *pituitary* body, the *tonsils*. The solitary and agminate glands (Peyer's) of the intestine, and lymph-glands in general, also closely resemble them; indeed, both in structure and function, the vascular glands bear a close relation, on the one hand, to the true secreting glands, and on the other, to the lymphatic glands. The evidence in favour of the view that these organs exercise a function analogous to that of secreting glands, has been chiefly obtained from investigations into their structure, which have shown that most of the glands without ducts contain the same essential structures as the secreting glands, except the ducts.

The Spleen.

The Spleen is the largest of the so-called ductless glands; it is situated to the left of the stomach, between it and the diaphragm. It is of a deep red colour, of a variable shape, generally oval, somewhat concavo-convex. Vessels enter and leave the spleen at the inner side (hilus).

Structure.—The spleen is covered externally almost completely by a serous coat derived from the peritoneum, while within this is the proper fibrous coat or capsule of the organ. The latter, composed of connective tissue, with a large preponderance of elastic fibres, and a certain proportion of unstriated muscular tissue, forms the immediate investment of the spleen. Prolonged from its inner surface are fibrous processes or *trabeculæ*, containing much unstriated muscle, which enter the interior of the organ, and, dividing and anastomosing in all parts, form a kind of supporting frame-work or *stroma*, in the interstices of which the proper substance of the spleen (*spleen-pulp*) is contained (fig. 254). At the hilus of the spleen, the blood-vessels, nerves, and lymphatics enter, and the fibrous coat is prolonged into the

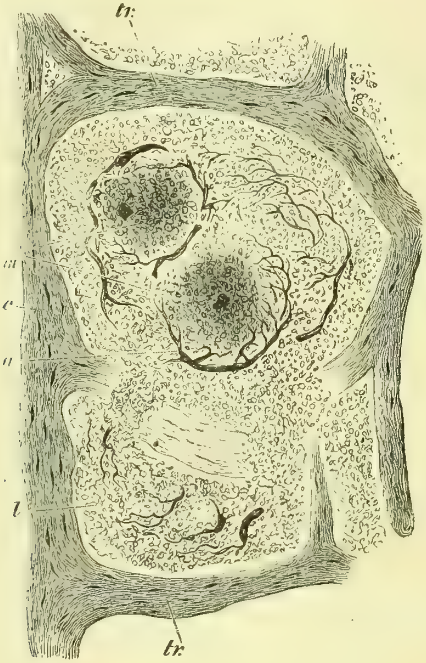


Fig 254.—*Section of dog's spleen injected:* *c*, capsule; *tr*, trabeculæ; *m*, two Malpighian bodies with numerous small arteries and capillaries; *a*, artery; *l*, lymphoid tissue, consisting of closely-packed lymphoid cells supported by very delicate retiform tissue; a light space unoccupied by cells is seen all round the trabeculæ, which corresponds to the "lymph path" lymphatic glands (Schofield).

spleen-substance in the form of investing sheaths for the arteries and veins, which sheaths again are continuous with the *trabeculæ* before referred to.

The *spleen-pulp*, which is a dark red or reddish-brown colour, is composed chiefly of cells, imbedded in a matrix of fibres formed of the branchings of large flattened nucleated endotheloid cells. The spaces of the network only partially occupied by cells form a freely communicating system. Of the cells some are granular corpuscles resembling the lymph-corpuscles, more or less connected with the cells of the meshwork, both in general appearance and in being able to perform amœboid movements; others are red blood-corpuscles of normal appearance or variously changed; while there are also large cells containing either a pigment allied to the colouring matter of the blood, or rounded corpuscles like red blood-cells.

The splenic artery, after entering the spleen by its concave surface, divides and subdivides, with but little anastomosis between its branches; at the same time its branches are sheathed by the prolongations of fibrous coat, which they, so to speak, carry into the spleen with them. The arteries send off branches into the spleen-pulp which end in capillaries, and these either communicate, as in other parts of the body, with the radicles of the veins, or end in lacunar spaces in the spleen-pulp, from which veins arise (Gray).

The walls of the smaller veins are more or less incomplete, and readily allow lymphoid corpuscles to be swept into the blood-current. "The blood traverses the network of the pulp, and interstices of the lymphoid cells contained in the latter, in the same manner as the water of a river finds its way among the pebbles of its bed: the blood from the arterial capillaries is emptied into a system of intermediate passages, which are directly bounded by the cells and fibres of the network of the pulp, and from which the smallest venous radicles with their cribriform walls take origin" (Frey). The veins are large and very distensible: the whole tissue of the spleen is highly vascular, and becomes readily engorged with blood: the amount of distension is, however, limited by the fibrous and muscular tissue of its capsule and trabeculæ, which forms an investment and support for the pulpy mass within.

On the face of a section of the spleen can be usually seen readily with the naked eye, minute, scattered rounded or oval whitish spots, mostly from $\frac{1}{30}$ to $\frac{1}{60}$ inch in diameter. These are the *Malpighian corpuscles* of the spleen, and are situated on the sheaths of the minute splenic arteries, of which, indeed, they may be said to be outgrowths (fig. 254). For while the sheaths of the larger arteries are constructed of ordinary connective tissue, this has become modified where it forms an investment for the smaller vessels, so as to be composed of adenoid tissue, with abundance of corpuscles, like lymph-corpuscles, contained in its meshes, and the Malpighian corpuscles are but small outgrowths of this *cytogenous* or cell-bearing connective tissue. They are composed of cylindrical masses of corpuscles, intersected in all parts by a delicate fibrillar tissue, which though it invests the Malpighian bodies, does not form a complete capsule. Blood-capillaries traverse the Malpighian corpuscles and form a plexus in their interior. The structure of a Malpighian corpuscle of the spleen is, therefore, very similar to that of lymphatic-gland substance.

Functions.—With respect to the office of the spleen, we have the following data. (1.) The large size which it gradually acquires towards the termination of the digestive process, and the great increase observed about this period in the amount of the finely-granular albuminous plasma within its parenchyma, and the subsequent gradual decrease of this material, seem to indicate that this organ is concerned in elaborating the albuminous materials of food, and for a time storing them up, to be gradually introduced into the blood, according to the demands of the general system.

(2.) It seems probable that the spleen, like the lymphatic glands, is engaged in the formation of blood-corpuscles. For it is quite certain, that the blood of the splenic vein contains an unusually large amount of white corpuscles; and in the disease termed leucocythæmia, in which the pale corpuscles of the blood are remarkably increased in number, there is almost always found an hypertrophied state of the spleen or of the lymphatic glands. In Kölliker's opinion, the development of colourless and also coloured corpuscles of the blood is one of the essential functions of the spleen, into the veins of which the new-formed corpuscles pass, and are thus conveyed into the general current of the circulation.

(3.) There is reason to believe, that in the spleen many of the red corpuscles of the blood, those probably which have discharged their office and are worn out, undergo disintegration; for in the coloured portions of the spleen-pulp an abundance of such corpuscles, in various stages of degeneration, are found, while the red corpuscles in the splenic venous blood are said to be relatively diminished. This process appears to be as follows. The blood-corpuscles, becoming smaller and darker, collect together in roundish heaps, which may remain in this condition, or become each surrounded by a cell-wall. The cells thus produced may contain from one to twenty blood-corpuscles in their interior. These corpuscles become smaller and smaller; exchange their red for a golden yellow, brown, or black colour; and at length, are converted into pigment-granules, which by degrees become paler and paler, until all colour is lost. The corpuscles undergo these changes whether the heaps of them are enveloped by a cell-wall or not.

(4.) From the almost constant presence of uric acid, as well as of the nitrogenous bodies, xanthin, hypoxanthin, and leucin, in the spleen, some nitrogenous metabolism may be fairly inferred to occur in it.

(5.) Besides these, its supposed direct offices, the spleen is believed to fulfil some purpose in regard to the portal circulation, with which it is in close connection. From the readiness with which it admits of being distended, and from the fact that it is generally small while gastric digestion is going on, and enlarges when that act is concluded, it is supposed to act as a kind of vascular reservoir, or diverticulum to the portal system, or more particularly to the vessels of the stomach. That it may serve such a purpose is also made probable by the enlargement which it undergoes in certain affections of the heart and liver, attended with obstruction to the passage of blood through the latter organ, and by its diminution when the congestion of the portal system is relieved by discharges from the bowels, or by the effusion of blood into the stomach. This mechanical influence on the circulation, however, can hardly be supposed to be more than a very subordinate function.

It is only necessary to mention that Schiff believes that the spleen manufactures a substance without which the pancreatic secretion cannot act upon proteids, so that when the spleen is removed the digestive action of the pancreas is stopped.

Influence of the Nervous System upon the Spleen.—When the spleen is enlarged after digestion, its enlargement is probably due to two causes, (1) a relaxation of the muscular tissue which forms so large a part of its framework; (2) a dilatation of the vessels. Both these phenomena are doubtless under control of the nervous system. It has been found by experiment that when the splenic nerves are cut the spleen enlarges, and that contraction can be brought about (1) by stimulation of the spinal cord (or of the divided nerves); (2) reflexly by stimulation of the central stumps of certain divided nerves, *e.g.*, vagus and sciatic; (3) by local stimulation by an electric current; (4) the exhibition of quinine and some other drugs. It has been shown by means of a modification of the plethysmograph (Roy), that the spleen undergoes rhythmical contractions and dilatations, due no doubt to the contraction and relaxation of the muscular tissue in its capsule and trabeculæ. The gland also shows the rhythmical alteration of the general blood pressure but to a less extent than the kidney.

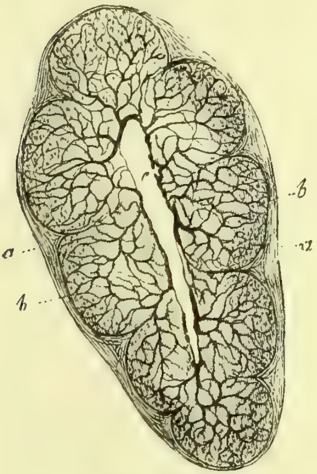


Fig. 255.—*Transverse section of a lobule of an injected infantile thymus gland.* a, capsule of connective-tissue surrounding the lobule; b, membrane of the glandular vesicles; c, cavity of the lobule, from which the larger blood-vessels are seen to extend towards and ramify in the spheroidal masses of the lobule. × 30. (Kölliker.)

The Thymus.

This gland must be looked upon as a temporary organ, as it attains its greatest size early after birth, and after the second year gradually diminishes, until in adult life hardly a vestige remains. At its greatest development it is a long narrow body, situated in the front of the chest behind the sternum and partly in the lower part of the neck. It is of a reddish or greyish colour, distinctly lobulated.

Structure.—The gland is surrounded by a fibrous capsule which sends in processes, forming trabeculæ, which divide the gland into lobes, and carry the blood- and lymph-vessels. The large trabeculæ branch into small ones, which divide the lobes into lobules. The gland is encased in a fold of the pleura. The lobules are further subdivided into follicles by fine connective tissue. A follicle (fig. 256) is more or less polyhedral in shape, and consists of cortical and medullary portions, the structure of both being of adenoid tissue, but in the medullary portion the matrix is coarser, and is not so filled up with lymphoid corpuscles as in the cortex. The adenoid tissue of the cortex, and to a less marked extent in the medulla, consists of two kinds of tissue, one with small meshes formed of fine fibres with thickened nodal points, and the other enclosed within the first, composed of branched connective tissue corpuscles (Watney). Scattered in the adenoid tissue of the medulla are the *concentric corpuscles of Hassall*, which are protoplasmic masses of various sizes, consisting of a central nucleated granular centre, surrounded by flattened nucleated endothelial cells. In the reticulum, especially of the medulla, are large transparent giant cells. In the thymus of the dog and of other animals are to be found cysts, probably derived from the concentric corpuscles, some of which are lined with ciliated epithelium, and others with short columnar cells. Hæmoglobin is found in the thymus of all animals, either in these cysts, or in cells near to or of the concentric corpuscles. In the lymph issuing from the thymus are found cells containing coloured blood corpuscles and hæmoglobin granules, and in the lymphatics of the thymus there are more colourless cells than in the lymphatics of the neck. In the blood of the thymic vein, there appears sometimes to be an increase in the colourless corpuscles and also masses of granular matter (corpuscles of Zimmermann) (Watney). The arteries radiate from the centre of the gland. Lymph

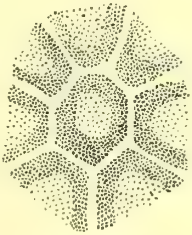


Fig. 256.—*From a horizontal section through superficial part of the thymus of a calf*, slightly magnified. Showing in the centre a follicle of polygonal shape with similarly shaped follicles round it (Klein and Noble Smith).

sinuses may be seen occasionally surrounding a greater or smaller portion of the periphery of the follicles (Klein). The nerves are very minute.

Function.—The thymus appears to take part in producing coloured corpuscles, both from the large corpuscles containing hæmoglobin, and also indirectly from the colourless corpuscles (Watney). Respecting the function of the gland in the hybernating animals, in which it exists throughout life; as each successive period of hybernation approaches, the thymus greatly enlarges and becomes laden with fat, which accumulates in it and in fat-glands connected with it, in even larger proportions than it does in the ordinary seats of adipose tissue. Hence it appears to serve for the storing up of materials which, being re-absorbed in inactivity of the hybernating period, may maintain the respiration and the temperature of the body in the reduced state to which they fall during that time.

The Thyroid.

The Thyroid gland is situated in the neck. It consists of two lobes one on each side of the trachea extending upwards to the thyroid cartilage, covering its inferior cornu and part of its body; these lobes are connected across the middle line by a middle lobe or isthmus. The thyroid is covered by the muscles of the neck. It is highly vascular, and varies in size in different individuals.

Structure.—The gland is encased in a thin transparent layer of dense areolar tissue, free from fat, containing elastic fibres. This capsule sends in strong fibrous trabeculæ, which enclose the thyroid *vesicles*—which are rounded or oblong irregular sacs, consisting of a wall of thin hyaline membrane lined by a single layér of low cylindrical or cubical cells. These vesicles are filled with a coagulable fluid or transparent colloid material. The colloid substance increases with age, and the cavities appear to coalesce. In the interstitial connective tissue is a round meshed capillary plexus and a large number of lymphatics. The nerves adhere closely to the vessels.

In the vesicles there are in addition to the yellowish glassy colloid material, epithelium cells, colourless blood corpuscles, and also coloured corpuscles undergoing disintegration.

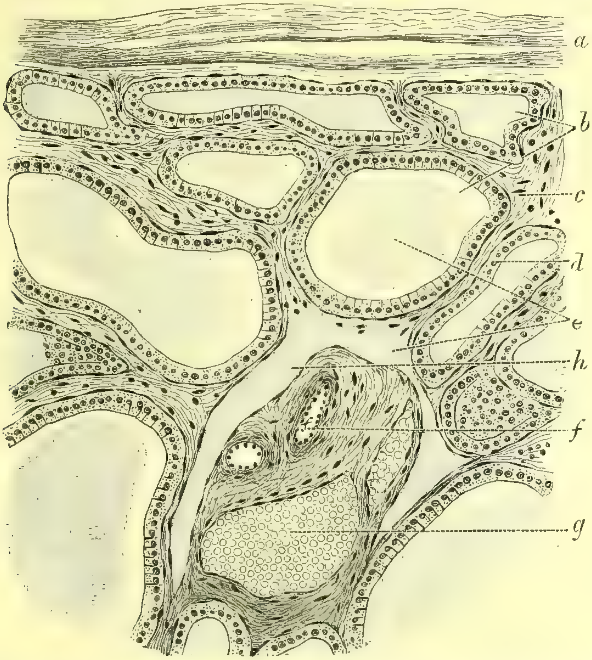


Fig. 257.—*Part of a section of the human Thyroid.* *a*, fibrous capsule; *b*, thyroid vesicles filled with, *e*, colloid substance; *c*, supporting fibrous tissue; *d*, short columnar cells lining vesicles; *f*, arteries; *g*, veins filled with blood; *h*, lymphatic vessel filled with colloid substance. (S. K. Alcock).

Function.—There is little known definitely about the function of the thyroid body. It, however, produces the colloid material of the vesicles, which is carried off by the lymphatics and discharged into the blood, and so may contribute its share to the elaboration of that fluid. The destruction of red blood-corpuscles is also supposed to go on in the gland.

Supra-renal Capsules or Adrenals.

These are two flattened, more or less triangular or cocked-hat shaped bodies, resting by their lower border upon the upper border of the kidneys.

Structure.—The gland is surrounded by an outer sheath of connective tissue, which sometimes consists of two layers, sending in exceedingly fine prolongations forming the framework of the gland. The gland tissue proper consists of an outside firmer cortical portion, and an inside soft dark medullary portion. (1.) The *cortical portion* is divided into (fig. 258b) an external narrow layer of small rounded or oval spaces, the *zona glomerulosa*, made by the fibrous trabeculæ, containing multinucleated masses of protoplasm, the differentiation of which into distinct cells cannot be made out. (*b*) A layer of cells arranged radially, the *zona fasciculata* (*c*). The substance of this layer is broken up into cylinders, each of which is surrounded by the connective tissue framework. The cylinders thus produced are of three kinds—one containing an opaque, resistant, highly refracting mass (probably of a fatty nature); frequently a large number of nuclei are present; the individual cells can only be made out with difficulty. The second variety of cylinders is of a brownish colour, and contains finely granular cells, in which are fat globules. The third variety consists of grey cylinders, containing a number of cells whose nuclei are filled with a large number of fat granules. The third

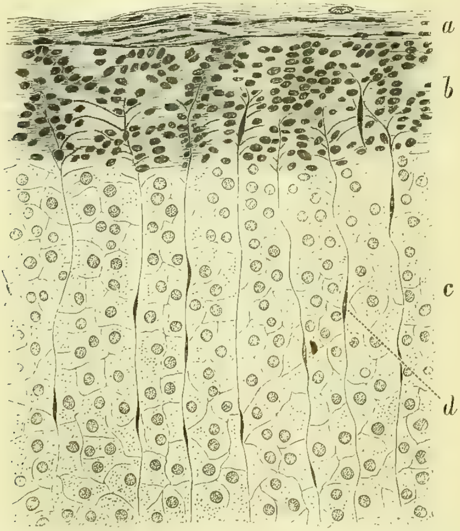


Fig. 258.—*Vertical section through part of the cortical portion of supra-renal of guinea-pig.* *a*, capsule; *b*, zona glomerulosa, *c*, zona fasiculata; *d*, connective tissue supporting the columns of the cells of the latter, and also indicating the position of the blood-vessels. (S. K. Alcock).

layer of the cortical portion is the *zona reticularis* (not shown in fig. 258). This layer is apparently formed by the breaking up of the cylinders, the elements being dispersed and isolated. The cells are finely granular, and have no deposit of fat in their interior; but in some specimens fat may be present, as well as certain large yellow granules, which may be called pigment granules.

(2.) The *medullary substance* consists of a coarse rounded or irregular meshwork of fibrous tissue, in the alveoli of which are masses of multinucleated protoplasm (fig. 259); numerous blood-vessels; and an abundance of nervous elements. The cells are very irregular in shape and size, poor in fat, and occasionally branched; the nerves run through the cortical substance, and anastomose over the medullary portion.

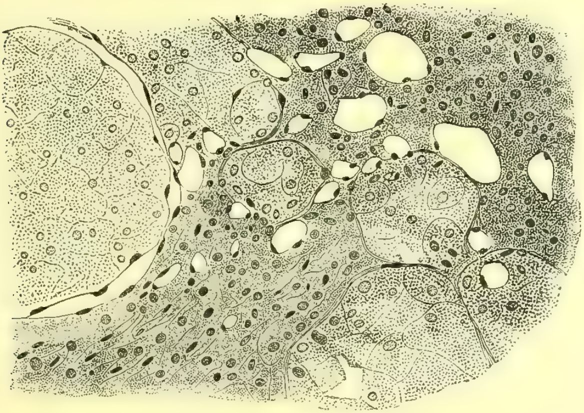


Fig. 259.—*Section through a portion of the medullary part of the supra-renal of guinea-pig.* The vessels are very numerous, and the fibrous stroma more distinct than in the cortex, and is moreover reticulated. The cells are irregular and larger, clean, and free from oil globules. (S. K. Alcock).

Function.—Of the function of the supra-renal bodies nothing can be definitely stated, but they are in all probability connected with the lymphatic system.

Addison's Disease.—The collection of large numbers of cases in which the supra-renal capsules have been diseased, has demonstrated the very close relation subsisting between disease of those organs and brown discoloration of the skin (Addison's disease); but the explanation of this relation is still involved in obscurity, and consequently does not aid much in determining the functions of the supra-renal capsules.

Pituitary Body.

This body is a small reddish-grey mass, occupying the sella turcica of the sphenoid bone.

Structure.—It consists of two lobes—a small posterior one, consisting of nervous tissue; an anterior larger one, resembling the thyroid in structure. A canal lined with flattened or with ciliated epithelium, passes through the anterior lobe; it is connected with the infundibulum. The gland spaces are oval, nearly round at the periphery, spherical towards the centre of the organ; they are filled with nucleated cells of various sizes and shapes not unlike ganglion cells, collected together into rounded masses, filling the vesicles, and contained in a semi-fluid granular substance. The vesicles are enclosed by connective tissue, rich in capillaries.

Function.—Nothing is known of the function of the pituitary body.

Pineal Gland.

This gland, which is a small reddish body, is placed beneath the back part of the corpus callosum, and rests upon the corpora quadrigemina (fig. 327, *g*).

Structure.—It contains a central cavity lined with ciliated epithelium. The gland substance proper is divisible into—(1.) An outer cortical layer, analogous in structure to the anterior lobe of the pituitary body; and (2) An inner central layer, wholly nervous. The cortical layer consists of a number of closed follicles, containing (*a*) cells of variable shape, rounded, elongated, or stellate; (*b*) fusiform cells. There is also present a gritty matter (*acervulus cerebri*), consisting of round particles aggregated into small masses. The central substance consists of white and grey matter. The blood-vessels are small, and form a very delicate capillary plexus.

Function.—Of this there is nothing known.

Functions of the Vascular Glands in General.

The opinion that the vascular glands serve for the higher organization of the blood, is supported by their being all especially active in the discharge of their functions during fœtal life and childhood, when, for the development and growth of the body, the most abundant supply of highly organised blood is necessary. The bulk of the thymus gland, in proportion to that of the body, appears to bear almost a direct proportion to the activity of the body's development and growth, and when, at the period of puberty, the development of the body may be said to be complete, the gland wastes, and finally disappears. The thyroid gland and supra-renal capsules, also, though they probably never cease to discharge some amount of function, yet are proportionally much smaller in childhood than in fœtal life and infancy ; and with the years advancing to the adult period, they diminish yet more in proportionate size and apparent activity of function. The spleen more nearly retains its proportionate size, and enlarges nearly as the whole body does.

The vascular glands seem not essential to life, at least not in the adult. The thymus wastes and disappears : no signs of illness attend some of the diseases which wholly destroy the structure of the thyroid gland ; and the spleen has been often removed in animals, and in a few instances in men, without any evident ill-consequence. It is possible that, in such cases, some compensation for the loss of one of the organs may be afforded by an increased activity of function in those that remain.

Although the functions of all the vascular glands may be similar, in so far as they may all alike serve for the elaboration and maintenance of the blood, yet each of them probably discharges a peculiar office, in relation either to the whole economy, or to that of some other organ. Respecting the special office of the thyroid gland, nothing reasonable can be suggested ; nor is there any certain evidence concerning that of the supra-renal capsules. Bergman believed that they formed part of the sympathetic nervous system from the richness of their nervous supply. Kölliker states that he is inclined to look upon the two parts as functionally distinct, the cortical part belonging to the blood vascular system, and the medullary to the nervous system.

CHAPTER XV.

CAUSES AND PHENOMENA OF MOTION.

In the animal body, motion is produced in these several ways: (1.) The oscillatory or vibratory movement of *Cilia.* (2.) *Amœboid* and certain *Molecular* movements. (3.) The contraction of *Muscular fibre.*

I. Ciliary Motion.

Ciliary, which is closely allied to amœboid and muscular motion (p. 9), consists in the incessant vibration of fine, pellucid processes, about $\frac{1}{5000}$ of an inch long, termed *cilia* (figs. 260, 261), situated on the free extremities of the cells of epithelium covering certain surfaces of the body.

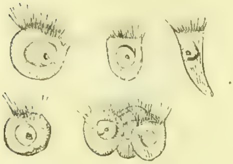


Fig. 260.—*Spheroidal ciliated cells from the mouth of the frog;* magnified 300 diameters. (Sharpey.)

The distribution and structure of ciliary epithelium and the microscopic appearances of cilia in motion have been already described (pp. 29, 30).

Ciliary motion is alike independent of the will, of the direct influence of the nervous system, and of muscular contraction. It continues for several hours after death or removal from the body, provided the portion of tissue under examination be kept moist. Its independence of the nervous system is shown also in its occurrence in the lowest invertebrate animals apparently unprovided with anything analogous to a nervous system, in its persistence in animals killed by prussic acid, by narcotic or other poisons, and after the direct application of narcotics to the ciliary surface, or the discharge of a Leyden jar, or of a galvanic shock through it. The vapour of chloroform arrests the motion; but it is renewed on the discontinuance of the application (Lister). The movement ceases in an atmosphere deprived of oxygen, but is revived on the

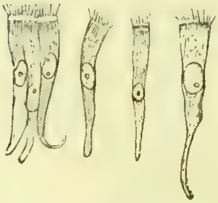


Fig. 261.—*Columnar ciliated cells from the human nasal membrane:* magnified 300 diameters. (Sharpey.)

admission of this gas. Carbonic acid stops the movement. The contact of various substances will stop the motion altogether; but this seems to depend chiefly on destruction of the delicate substance of which the cilia are composed.

Nature of Ciliary Action.—Little or nothing is known with certainty regarding the nature of ciliary action. It is a special manifestation of a similar property to that by which the other motions of animals are effected, namely, by what we term *vital contractility* (Sharpey). The fact of the more evident movements of the larger animals being effected by a structure apparently different from that of cilia, is no argument against such a supposition. For, if we consider the matter, it will be plain that our prejudices against admitting a relationship to exist between the two structures, muscles and cilia, rests on no definite ground; and for the simple reason, that we know so little of the manner of production of movement in either case. The mere difference of structure is not an argument in point; neither is the presence or absence of nerves. For in the fœtus the heart begins to pulsate when it consists of a mass of embryonic cells, and long before either muscular or nervous tissue has been differentiated. The movements of both muscles and cilia are manifestations of *energy*, by certain special structures, which we call respectively muscles and cilia. We know nothing more about the means by which the manifestation is effected by one of these structures than by the other: and the mere fact that one has nerves and the other has not, is no more argument against cilia having what we call a vital power of contraction, than the presence or absence of stripes from voluntary or involuntary muscles respectively, is an argument for or against the contraction of one of them being vital and the other not so.

As a special sub-division of ciliary action may be mentioned the motion of spermatozoa (fig. 403), which may be regarded as cells with a single cilium.

II. Amœboid Motion.

The remarkable movements observed in colourless blood corpuscles, connective tissue corpuscles, and many other cells (p. 9), must be regarded as depending on a kind of contraction of portions of their mass very similar to muscular contraction.

There is certainly an analogy between the spherical form assumed by a colourless blood-corpuscle on electric stimulation and the condition known as tetanus in muscles.

III. Muscular Motion.

Varieties of Muscular Tissue.—There are two chief kinds of muscular tissue: (1.) the *plain* or *non-striated*, and (2.) the *striated*, and they are distinguished by structural peculiarities and mode of action. The striped form of muscular fibre is sometimes called *voluntary* muscle, because all muscles under the direct control of the will are constructed of it. The plain or unstriped variety is often termed *involuntary*, because it alone is found in the greater number of the muscles over which the will has no power.

(1.) Plain or Unstriped Muscle.

Distribution.—Involuntary muscle forms the proper muscular coats (1.) of the digestive canal from the middle of the œsophagus to the internal sphincter ani; (2.) of the ureters and urinary bladder; (3.) the trachea and bronchi; (4.) the ducts of glands; (5.) the gall-bladder; (6.) the vesiculæ seminales; (7.) the pregnant uterus; (8.) of blood-vessels and lymphatics; (9.) the iris, and some other parts. This form of tissue also enters (10.) largely into the composition of the tunica dartos, and is the principal cause of the wrinkling and contraction of the scrotum on exposure to cold. Unstriped muscular tissue occurs largely also (11.) in the cutis (p. 413), being especially abundant in the interspaces between the bases of the papillæ. Hence when it contracts under the influence of cold, fear, electricity, or any other stimulus, the papillæ are made unusually prominent, and give rise to the peculiar roughness of the skin termed *cutis anserina*, or goose skin. It occurs also in the superficial portion of the cutis, in all parts where hairs occur, in the form of flattened roundish bundles, which lie alongside the hair-follicles and sebaceous

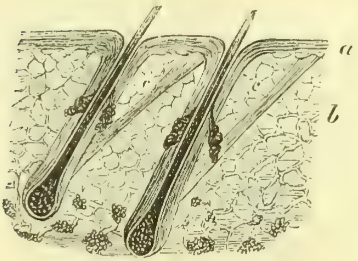


Fig. 262.—*Vertical section through the scalp with two hair-sacs;* *a*, epidermis; *b*, cutis; *c*, muscles of the hair-follicles (Kölliker).

glands. They pass obliquely from without inwards, embrace the sebaceous glands, and are attached to the hair-follicles near their base (fig. 228).

Structure.—The non-striated muscles are made up of elongated, spindle-shaped, nucleated *fibre cells* (fig. 263), which in their perfect form are flat, from about $\frac{1}{4500}$ to $\frac{1}{3500}$ of an inch broad, and $\frac{1}{600}$ to $\frac{1}{300}$ of an inch in length,—very clear, granular, and brittle, so that when they break they often have abruptly rounded or square extremities. Each *muscle cell* consists of a fine sheath, probably elastic; of a central bundle of fibrils representing the contractile substance; and of an oblong nucleus

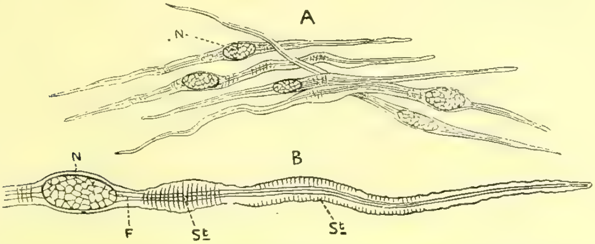


Fig. 263.—A, *unstriped muscle cells from mesentery of newt*, sheath with transverse marking faintly seen. × 180. B, from similar preparation, showing each muscle cell consists of a central bundle of fibrils (contractile part) connected with the intranuclear network and a sheath with annular thickenings. The cells show varicosities due to local contraction and on these the annular thickenings are most marked. × 450. (Klein and Noble Smith.)

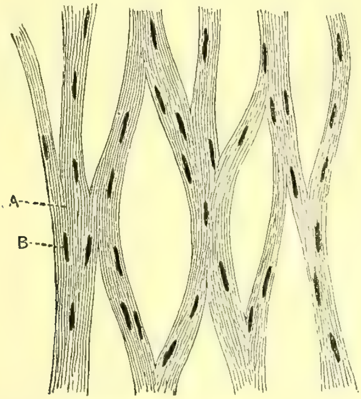


Fig. 264.—*Plexus of bundles of unstriped muscle cells of the pulmonary pleura* of the guinea-pig. × 180. (Klein and Noble Smith.)

which includes within a membrane a fine network anastomosing at the poles of the nucleus with the contractile fibrils. The ends of fibres are usually single, sometimes divided. Between the fibres is an albuminous cementing material (endomysium) in which are found connective tissue corpuscles, and a few fibres. The *perimysium* is the fibrous connective tissue surrounding and separating the bundles of muscle cells.

(2.) Striated or Striped Muscle.

Distribution.—The striated muscles include the whole class of *voluntary* muscles, the *heart*, and those muscles neither completely voluntary nor involuntary, which form part of the walls of the pharynx, and exist in many other parts of the body, as the internal ear, urethra, &c.

Structure.—All these muscles are composed of larger or smaller bundles of muscular fibres called *fasciculi*, enclosed in coverings of fibro-cellular tissue (*perimysium*), by which each is at once connected with and isolated from those adjacent to it (fig. 265). Supporting the fibres contained in each fasciculus is a scanty amount of fine connective tissue (*endomysium*).

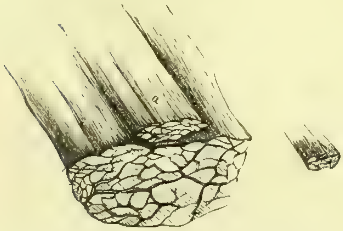


Fig. 265.—*A small portion of muscle natural size, consisting of larger and smaller fasciculi,* seen in a transverse section, and the same magnified 5 diameters (Sharpey).

Each muscular fibre is thus constructed :—Externally is a fine, transparent, structureless membrane, called the *sarcolemma* (fig. 266, A), which in the form of a tubular investing sheath forms the outer wall of the fibre, and is filled up by the contractile material of which the fibre is chiefly composed. Sometimes, from its comparative toughness, the sarcolemma will remain untorn, when by extension the contained part can be broken (fig. 269), and its presence is in this way best demonstrated. The fibres, which are cylindriform or prismatic, with an average diameter of about $\frac{1}{500}$ of an inch, are of a pale yellow colour, and apparently marked by fine striæ, which pass transversely round them, in slightly curved or wholly parallel lines. Each fibre is found to consist of broad dim bands of highly refractive substance representing the contractile portion of the muscle fibre—the *contractile discs* (fig. 267, A, *c*)—alternating with narrow bright bands of a less refractive substance—the *interstitial discs* (fig. 267, A, *i*). After hardening, each contractile disc becomes longitudinally striated, the thin oblong rods thus formed being the *sarcous elements* of Bowman. The sarcous elements are not the optical units, since each consists of minute doubly-refracting elements — the *disdiaclasts* of Brucke. When seen in transverse section the contractile discs appear to be subdivided by clear lines into polygonal areas *Cohnheim's fields* (fig. 271), each corresponding to one sarcous element prism. The clear lines are due to a transparent interstitial fluid substance pressed out of the sarcous elements when they coagulate. There is still some doubt regarding the nature of the fibrils. Each of them appears to be composed of a single row of minute dark quadrangular particles, called *sarcous elements*, which are separated from each other by a bright space formed of a pellucid substance continuous with them. Sharpey believes that, even in a fibril so constituted, the ultimate anatomical element of the fibre has not been isolated. He believes that each fibril with quadrangular sarcous elements is composed of a number of other fibrils still finer, so that the sarcous element of an ultimate fibril, would be not quadrangular but as a streak. In either case the appearance of striation in the whole fibre would be produced by the arrangement, side by side, of the dark and light portions respectively of the fibrils (fig. 267, B, *d*).

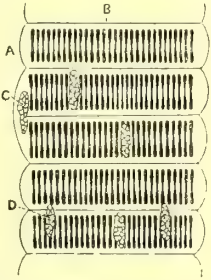


Fig. 266.—*Part of a striped muscle-fibre of a water-beetle* (hydrophilus) prepared with absolute alcohol. A, sarcolemma; B, Krause's membrane. Owing to contraction during hardening, the sarcolemma shows regular bulgings. Above and below Krause's membrane are seen the transparent "lateral discs." The chief mass of a muscular compartment is occupied by the contractile disc composed of sarcous elements. The substance of the individual sarcous elements has collected more at the extremity than in the centre: hence this latter is more transparent. The optical effect of this is that the contractile disc appears to possess a "median disc" (Disc of Hensen). Several nuclei of muscle corpuscles, C and D, are shown, and in them a minute network. × 300. (Klein and Noble Smith.)

A fine streak can usually be discerned passing across the interstitial disc between the sarcous elements : this streak is termed

Krause's membrane : it is continuous at each end with the sarcolemma investing the muscular fibre (fig. 266, B).

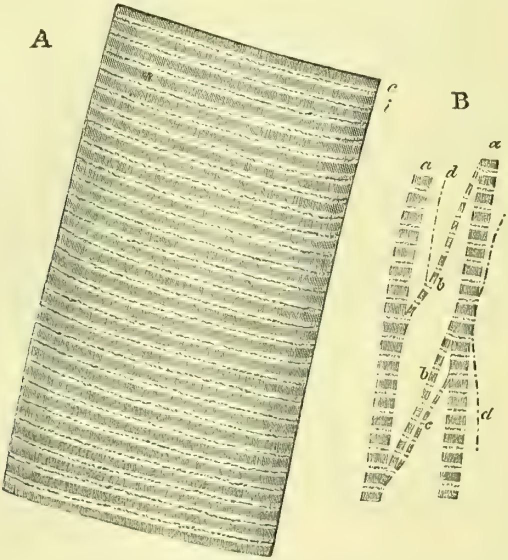


Fig. 267.—A. *Portion of a medium-sized human muscular fibre.* × 800. B. *Separated bundles of fibrils* equally magnified ; *a*, *a*, larger, and *b*, *b*, smaller collections ; *c*, still smaller ; *d*, *d*, the smallest which could be detached, possibly representing a single series of sarcous elements (Sharpey).

Thus the space enclosed by the sarcolemma is divided into a series of compartments by the transverse partitions known as Krause's membranes; these compartments being occupied by the true muscle substance. On each side (above and below) of Krause's membrane is a bright border (lateral disc). In the centre of the dark zone of sarcous elements a lighter band can sometimes be dimly discerned : this is termed the *middle disc of Hensen* (see fig. 266, A).

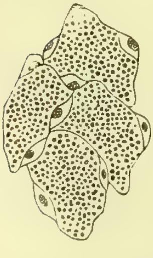


Fig. 268.— *Transverse section of a muscle-fibre of water-beetle* (hydrophilus piceus), showing the position of the muscle nuclei (Walter Pye).

In some fibres, chiefly those from insects, each lateral disc contains a row of bright granules forming the *granular layer* of Flögel. The fibres contain nuclei, which are roundish ovoid, or spindle-shaped in different animals. These nuclei are situated close to the sarcolemma, their long axes being parallel to the fibres which contain them. Each nucleus is composed of a uniform network of fibrils,

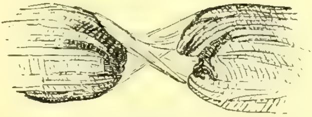


Fig. 269.—*Muscular fibre torn across;* the sarcolemma still connecting the two parts of the fibre (Todd and Bowman).

and is embedded in a thin, more or less branched film of protoplasm. The nucleus and protoplasm together form the muscle cell or *muscle corpuscle* of Max Schultze.

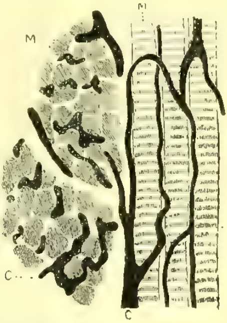


Fig. 270.—*Section through the muscular substance of the tongue, with capillaries injected,* their meshes running parallel to the fibres. Three muscular fibres are seen running longitudinally, and two bundles of fibres in transverse section. × 150. (Klein and Noble Smith.)

The sarcous elements and Krause's membranes are doubly refracting, the rest of the fibre singly refracting (Brücke).

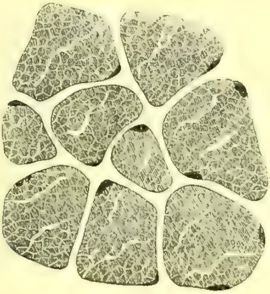


Fig. 271.—*Transverse section through muscular fibres of human tongue;* the fibres appear in transverse section of different sizes owing to their being more or less spindle-shaped. The muscle-corpuscles are indicated by their deeply-stained nuclei situated at the inside of the sarcolemma. Each muscle-fibre shows the "Cohnheim's fields," that is the sarcous elements in transverse section separated by clear (apparently linear) interstitial substance. × 450. (Klein and Noble Smith.)

According to Schäfer, the granules, which have been mentioned on either side of Krause's membrane, are little knobs attached to the ends of "muscle-rods;" and these muscle-rods, knobbed at each end and imbedded in a homogeneous protoplasmic ground-substance, form the substance of the muscles. This view, however, of the structure of muscle requires further confirmation before it can be accepted.

Although each muscular fibre may be considered to be formed of a number of longitudinal fibrils, arranged side by side, it is also true that they are not naturally separate from each other, there being *lateral* cohesion, if not fusion, of each sarcous element with those around and in contact with it; so that it happens that there is a tendency for a fibre to split, not only into separate fibrils, but also occasionally into plates or disks, each of which is composed of sarcous elements laterally adherent one to another.

Muscular Fibres of the Heart (figs. 272 and 273) form the chief, though not the only exception to the rule, that involuntary muscles are constructed of *plain* fibres; but although striated and so far resembling those of the skeletal muscles, they present these distinctions :—Each muscular fibre is made up of elongated,

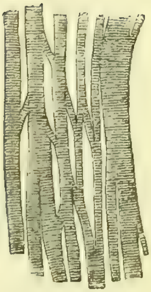


Fig. 272.—*Muscular fibres from the heart*, magnified, showing their cross-striæ, divisions, and junctions (Kölliker).

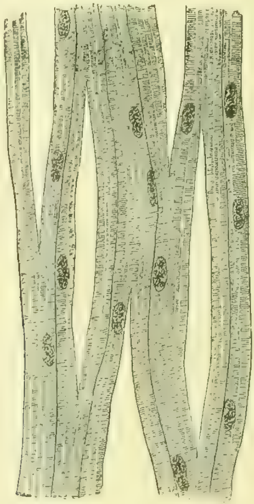


Fig. 273.—*Network of muscular fibres* (striated) from the heart of a pig. The nuclei of the muscle-corpuscles are well shown. × 450. (Klein and Noble Smith.)

nucleated, and branched cells, the nuclei or muscle-corpuscles being centrally placed in the fibre. The fibres are finer and less distinctly striated than those of the voluntary muscles; and no sarcolemma can be usually discerned.

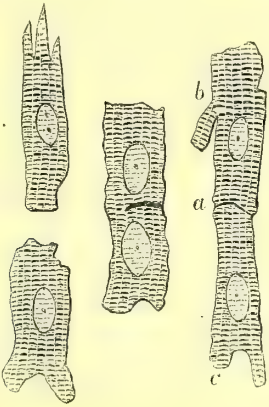


Fig. 274.—*Muscular fibre cells from the heart.* (E. A. Schäfer.)

Blood and Nerve Supply.—The voluntary muscles are freely supplied with blood-vessels ; the capillaries form a network with oblong meshes around the fibres on the outside of the sarcolemma. No vessels penetrate the sarcolemma to enter the interior of the fibre (fig. 270). Nerves also are supplied freely to muscles (pp. 549, 554) ; the voluntary muscles receiving chiefly nerves from the cerebro-spinal system, and the unstriped muscles from the sympathetic or ganglionic system.

Development.—(1.) *Unstriped.*—The cells of unstriped muscle are derived directly from embryonic cells, by an elongation of the cell, and its nucleus ; the latter changing from a vesicular to a rod shape.

(2.) *Striped.*—Formerly it was supposed that striated fibres are formed by the coalescence of several cells, but recently it has been proved, that each fibre is formed from a single cell, the process involving an enormous increase in size, a multiplication of the nucleus by fission, and a differentiation of the cell-contents (Remak, Wilson Fox). This view differs but little from that previously taken by Savory, that the muscular fibre is produced, not by multiplication of cells, but by arrangement of nuclei in a growing mass of protoplasm (answering to the cell in the theory just referred to), which becomes gradually differentiated so as to assume the characters of a fully developed muscular fibre.

Growth of Muscle.—The growth of muscles, both striated and non-striated, is the result of an increase both in the number and size of the individual elements.

In the pregnant uterus the fibre-cells may become enlarged to ten times their original length. In involution of the uterus after parturition the reverse changes occur, accompanied generally by some fatty infiltration of the tissue and degeneration of the fibres.

Physiology of Muscle.

Muscle may exist in three different conditions; *rest*, *activity*, and *rigor*.

I. Rest.

Physical condition.—During rest or inactivity a muscle has a slight but very perfect *elasticity;* it admits of being considerably stretched; but returns readily and completely to its normal length. In the living body the muscles are always *stretched* somewhat beyond their natural length, they are always in a condition of slight tension; an arrangement which enables the whole force of the contraction to be utilised in approximating the points of attachment. It is obvious that if the muscles were lax, the first part of the contraction till the muscle became tight would be wasted.

There is no doubt that even in a condition of rest *oxygen* is being *abstracted from the blood* and carbonic acid given out by a muscle; for the blood becomes venous in the transit, and since the muscles form by far the largest element in the composition of the body, chemical changes must be constantly going on in them as in other tissues and organs, although not necessarily accompanied by contraction. When cut out of the body such muscles retain their contractility longer in an atmosphere of oxygen than in an atmosphere of hydrogen or carbonic acid, and during life, an amount of oxygen is no doubt necessary to the manifestation of energy as well as for the metabolism going on in the resting condition.

Chemical composition.—The reaction of living muscle is *neutral* or *slightly alkaline.* The substance or muscle plasma which forms the contractile principal element in its composition undergoes coagulation when the muscle is removed from the body, and the process may be observed if the coagulation be delayed by cold. If the muscles of a frog be frozen, minced whilst in that condition, and reduced to a pulp by being rubbed up with a 1 per cent. solution of sodium chloride, the temperature of which must be very low, on filtration in the cold, a colourless, somewhat turbid filtrate separates with difficulty, which is muscle plasma. This fluid at the ordinary temperature of the air undergoes a coagulation or clotting, by which it is separated, as in the case of blood, into *muscle-serum* and *muscle-clot.* The latter, however, is not made up of fibrin but of *myosin*, which is a globulin (p. 846). Myosin may also be obtained from dead muscle by subjecting it, after all the blood, fat, fibrous tissue, and substances soluble in water, have been removed, to a ten per cent. solution of sodium chloride, filtering and allowing the filtrate to drop into a large quantity of water; myosin separating out as a white flocculent precipitate. Obtained in either way, viz., from living or dead muscle, myosin is soluble in dilute saline solutions, and the solution undergoes coagulation at a lower temperature than serum-albumin or paraglobulin, viz., at 131°—140° F. (55°—60° C.). It is coagulated also by alcohol. It is dissolved and converted into acid-albumin by dilute acid, such as hydrochloric.

Muscle-serum is acid in reaction, contains serum-albumin and several other proteids as well as other bodies, among which are fats; free acids, especially sarco-lactic, formic, and acetic; glucose, glycogen and inosite; kreatin, hypoxanthin, or carnin, taurin, and other nitrogenous crystalline bodies; many salts, of which the chief is potassium phosphate; Carbonic acid, and lastly Hæmoglobin, on which the colour of muscles partially depends. There are also traces of ferments, pepsin among others.

Electrical Condition; Natural muscle currents.—In muscles which have been removed from the body, it has been found that electrical currents can be demonstrated for some little time, passing from point to point on their surface; but as soon as the muscles die or enter into rigor mortis, these currents disappear.

The method of demonstration usually employed is as follows: The frog's muscles are most convenient for experiment, and a muscle of regular shape, in which the fibres are parallel, is selected. The ends are cut off by clean vertical cuts, and the resulting piece of muscle is called a regular muscle prism. The muscle prism is insulated, and a pair of non-polarisable electrodes connected with a very delicate galvanometer are applied to various points of the prism, and by a deflection of the needle to a greater or less extent in one direction or another, the strength and direction of the currents in the piece of muscle can be estimated. It is necessary to use non-polarisable and not metallic electrodes in this experiment, as otherwise there is no certainty that the whole of the current observed is communicated from the muscle and is not derived from the metallic electrodes themselves in consequence of the action of the saline juices of the tissues upon them. The form of the non-polarisable electrodes is a modification of Du Bois Reymond's apparatus (fig. 275), which consists of a somewhat flattened glass cylinder *a*, drawn abruptly to a point and fitted to a socket capable of movement and attached to a stand A, so that it can be raised or lowered as required. The lower portion of the cylinder is filled with china clay moistened with saline solution, part of which projects through its drawn-

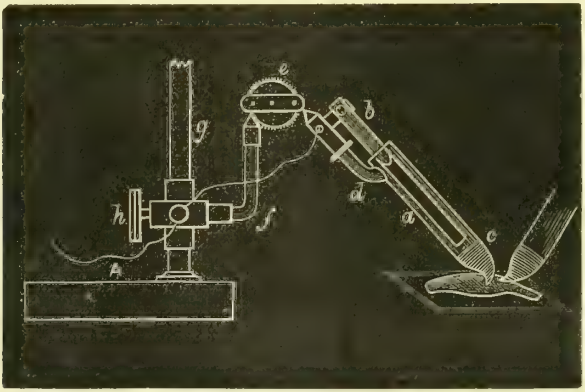


Fig. 275.—*Diagram of Du Bois Reymond's non-polarisable electrodes.* *a*, glass tube filled with a saturated solution of zinc sulphate, in the end, *c*, of which is china clay drawn out to a point; in the solution a well amalgamated zinc rod is immersed and connected by means of the wire which passes through A with the galvanometer. The remainder of the apparatus is simply for convenient application. The muscle to the end of the second electrode is to the right of the figure.

out point; the rest of the cylinder is fitted with a saturated solution of zinc sulphate into which dips a well amalgamated piece of zinc which is connected by means of a wire with the galvanometer. In this way the zinc sulphate forms an homogeneous and non-polarisable conductor between the zinc and the china clay. A second electrode of the same kind is, of course, necessary.

In such a regular muscle prism the currents are found to be as follows :—

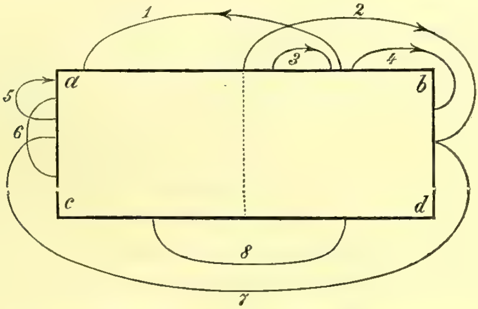


Fig. 276.—*Diagram of the currents in a muscle prism.* (Du Bois Reymond.)

If from a point on the surface a line—the equator—be drawn across the muscle prism equally dividing it, currents pass from this point to points away from it, which are weak if the points are near, and increase in strength as the points are further and further away from the equator; the strongest passing from the equator to a point representing the middle of the cut ends (fig. 276, 2); currents also pass from points nearer the equator to those more remote (fig. 276, 1, 3, 4), but not from points equally distant, or iso-electric points (fig. 276, 6, 7, 8). The cut ends are always negative to the equator. These currents are constant for some time after removal of the muscle from the body, and in fact remain as long as the muscle retains its life. They are in all probability due to chemical change going on in the muscles.

The currents are diminished by fatigue and are increased by an increase of temperature within natural limits. If the uninjured tendon be used as the end of the muscle, and the muscle be examined without removal from the body, the currents are very feeble, but they are at once much increased by injuring the muscle, as by cutting off its tendon. The last observation appears to show that they are right who believe that the currents do not exist in muscles uninjured *in situ*, but that injury, either mechanical, chemical or thermal, will render the injured part electrically negative to other points on the muscle. In a frog's heart it has been shown, too, that no currents exist during its inactivity, but that as soon as it is injured in any way currents are developed, the injured part being negative to the rest of the muscle. The currents which have been above described are called either *natural muscle currents* or *currents of rest*, according as they are looked upon as always existing in muscle or as developed when a part of the muscle is subjected to injury; in either case, up to a certain point, it is agreed that the strength of the currents is in direct proportion to the injury.

II. Activity.

The property of muscular tissue, by which its peculiar functions are exercised, is its *contractility*, which is excited by all kinds of stimuli applied either directly to the muscles, or indirectly to them through the medium of their motor nerves. This property, although commonly brought into action through the nervous system, is inherent in the muscular tissue. For—(1). it may be manifested in a muscle which is isolated from the influence of the nervous system by division of the nerves supplying it, so long as the natural tissue of the muscle is duly nourished; and (2). it is manifest in a portion of muscular fibre, in which, under the microscope, no nerve-fibre can be traced. (3). Substances such as *urari*, which paralyse the nerve-endings in muscles, do not at all diminish the irritability of the muscle. (4). When a muscle is fatigued, a local stimulation is followed by a contraction of a small part of the fibre in the immediate vicinity without any regard to the distribution of nerve-fibres.

If the removal of nervous influence be long continued, as by division of the nerves supplying a muscle, or in cases of paralysis of long-standing, the irritability, *i.e.*, the power of both perceiving and responding to a stimulus, may be lost; but probably this is chiefly due to the impaired nutrition of the muscular tissue, which ensues through its inaction. The irritability of muscles is also of course soon lost, unless a supply of arterial blood to them is kept up. Thus, after ligature of the main arterial trunk of a limb, the power of moving the muscles is partially or wholly lost, until the collateral circulation is established; and when, in animals, the abdominal aorta is tied, the hind legs are rendered almost powerless.

The same fact may be readily shown by compressing the abdominal aorta in a rabbit for about 10 minutes; if the pressure be released and the animal be placed on the ground, it will work itself along with its front legs, while the hind legs sprawl helplessly behind. Gradually the muscles recover their power and become quite as efficient as before.

So, also, it is to the imperfect supply of arterial blood to the muscular tissue of the heart, that the cessation of the action of this organ in asphyxia is in some measure due.

Sensibility.—Besides the property of contractility, the muscles, especially the striated, possess sensibility by means of the sensory nerve-fibres distributed to them. The amount of common sensibility in muscles is not great; for they may be cut or pricked without giving rise to severe pain, at least in their healthy condition. But they have a peculiar sensibility, or at least a peculiar modification of common sensibility, which is shown in that their nerves can communicate to the mind an accurate knowledge of their states and positions when in action. By this sensibility, we are not only made conscious of the morbid sensations of fatigue and cramp in muscles, but acquire, through muscular action, a knowledge of the distance of bodies and their relation to each other, and are enabled to estimate and compare their weight and resistance by the effort of which we are conscious in measuring, moving, or raising them. Except with such knowledge of the position and state of each muscle, we could not tell how or when to move it for any required action; nor without such a sensation of effort could we maintain the muscles in contraction for any prolonged exertion.

Muscular Contraction.

The power which muscles possess of contraction may be called forth by stimuli of various kinds, viz., by Mechanical, Thermal, Chemical, and Electrical means, and these stimuli may also be applied directly to the muscle or indirectly to the nerve supplying it. There are distinct advantages, however, in applying the stimulus through the nerves, as it is more convenient, as well as more potent.

Mechanical stimuli, as by a blow, pinch, prick of the muscle or its nerve, will produce a contraction, repeated on the repetition of the stimulus; but if applied to the same point for a limited number of times only, as such stimuli will soon destroy the irritability of the preparation.

Thermal stimuli.—If a needle be heated and applied to a muscle or its nerve, the muscle will contract. A temperature of over 100° F. (37·8° C.) will cause the muscles of a frog to pass into a condition known as *heat rigor.*

Chemical stimuli.—A great variety of chemical substances will excite the contraction of muscles, some substances being more potent in irritating the muscle itself, and other substances having more effect upon the nerve. Of the former may be mentioned, dilute acids, salts of certain metals, *e.g.*, zinc, copper and iron; to the latter belong strong glycerin, strong acids, ammonia and bile salts in strong solution.

Electrical stimuli.—These are most frequently used as muscle stimuli, as the strength of the stimulus may be more conveniently regulated. The kind of current employed may be, for the sake of clearness, treated of under two heads:—(1) *The continuous current*, and (2) *The induced current.* (1) The continuous current is supplied by a battery such as that of Daniell, by which an electrical current which varies but little in intensity is obtained. The

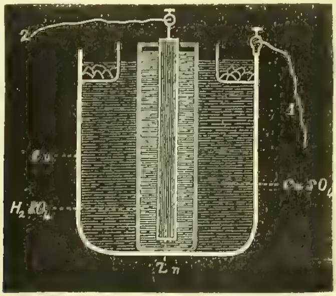


Fig. 277.—*Diagram of a Daniell's battery.* (After Balfour Stewart).

battery (fig. 277) consists of a positive plate of well-amalgamated zinc immersed in a porous cell, containing dilute sulphuric acid; and this cell is again contained within a larger copper vessel (forming the negative plate), containing besides a saturated solution of copper sulphate. The electrical current is made continuous by the use of the two fluids in the following manner. The action of the dilute sulphuric acid upon the zinc plate partly dissolves it and liberates hydrogen, and this gas passes through the porous vessel and decomposes the copper sulphate into copper and sulphuric acid. The former is deposited upon the copper plate and the latter passes through the porous vessel to renew the sulphuric acid which is being used up. The copper sulphate solution is renewed by spare crystals of the salt which are kept on a little shelf attached to the copper plate and slightly below the level of the solution in the vessel. The current of electricity supplied by this battery will continue without variation for a considerable time. Other continuous-current batteries such as Grove's may be used in place of Daniell's. The way in which the apparatus is arranged is to attach wires to the copper and zinc plates and to bring them to a key, which is a little apparatus for connecting the wires of a battery. One often employed is Du Bois Reymond's (fig. 280, D); it consists of two pieces of brass about an inch long, in each of which are two holes for wires and binding screws to fix them tightly; these pieces of brass are fixed upon a vulcanite plate, to the under surface of which is a screw clamp by which it can be secured to the table. The interval between the pieces of brass can be bridged over by means of a third thinner piece of similar metal fixed by a screw to one of the brass pieces and capable of movement by a handle at right angles, so as to touch the other piece of brass. If the wires from the battery are brought to the inner binding screws, and the bridge be brought to connect them, the current passes across it and back to the battery. Wires are connected with the outer binding screws, and the other ends are approximated for about two inches, but, being covered except at their points, are insulated, the uncovered points are about an eighth of an inch apart. These wires are the *electrodes*, and the electrical stimulus is applied to the muscle, if they are placed behind its nerve and the connection between the two brass plates of the key be broken by depressing the handle of the bridge and so raising the connecting piece of metal. The key is then said to be opened. (2) *The induced current.*—An induced current is developed by means of an apparatus called an *induction coil*, and the one employed for physiological purposes is mostly the one (fig. 278).

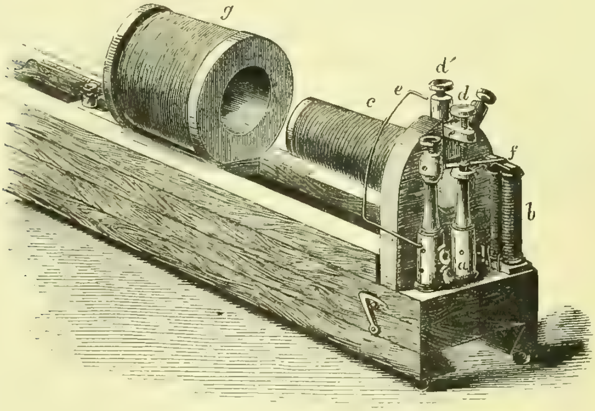


Fig. 278.—*Du Bois Reymond's induction coil.*

Wires from a battery are brought to the two binding screws *d′* and *d*, a key intervening. These binding screws are the ends of a coil of coarse covered wire *c*, called the primary coil. The ends of a coil of finer covered wire *g*, are attached to two binding screws to the left of the figure, one only of which is visible. This is the secondary coil and is capable of being moved nearer to *c* along a grooved and graduated scale. To the binding screws to the left of *g*, the wires of electrodes used to stimulate the muscle are attached. If the key in the circuit of wires from the battery to the primary coil (primary circuit) be closed, the current from the battery passes through the primary coil and across the key to the battery and continues to pass as long as the key continues closed. At the moment of closure of the key, at the exact instant of the completion of the primary circuit, an instantaneous current of electricity is induced in the secondary coil, *g*, if it be sufficiently near, and the nearer it is to *c*, the stronger is the current. The induced current is only momentary in duration and does not continue during the whole of the period when the primary circuit is complete. When, however, the primary current is broken by opening the key, a second, also momentary, current is induced in *g*. The former induced current is called the *making*, and the latter the *breaking* shock; the former is in the opposite to, and the latter in the same direction, as the primary current.

The induction coil may be used to produce a rapid series of shocks by means of another and accessory part of the apparatus at the right of the fig. If the wires from a battery are connected with the two pillars by the binding screws, one below *c*, and the other, *a*, the course of the current is indicated in fig. 279, the direction being indicated by the arrows. The current passes up the pillar from *e*, and along the spring, if the end of *d′* be close to the spring, and the current passes to the primary coil *c*, and to wires covering two upright pillars of soft iron, from them to the pillar *a*, and out by the wires to the battery; in passing along the wire, *b*, the soft iron is converted into a magnet and so attracts the hammer, *f*, of the spring, breaks the connection of the spring with *d′* and so cuts off the current from the primary coil and also from the electro-magnet. As the pillars, *b*, are no longer magnetized the spring is released and the current passes in the first direction, and is in like manner interrupted. At each make and break of the primary current, currents corresponding are induced in the secondary coil. These currents are, as before, in an opposite direction, but are not equal in intensity, the break shock being greater. In order that the shocks should be about equal at the make and break, a wire (fig. 279, *e′*) connects *e* and *d′*, and the screw *d′* is raised out of reach of the spring, and *d* is raised (as in fig. 279), so that part of the current always passes through the primary coil and electro-magnet. When the spring touches *d*, the current in *b* is diminished, but never entirely

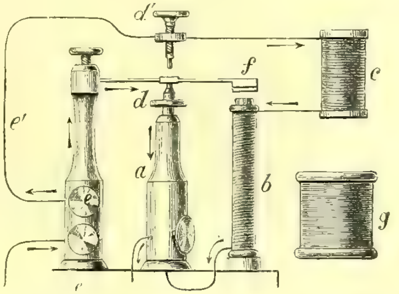


Fig. 279.—*Diagram of the course of the current in the magnetic interrupter of Du Bois Reymond's induction coil.* (Helmholz's modification.)

withdrawn, and the primary current is altered in intensity at each contact of the spring with *d*, but never entirely broken.

Record of Muscular Contraction under Stimuli.

The muscles of the frog are those which can most conveniently be experimented with and their contractions recorded. The frog is pithed, that is to say its central nervous system is entirely destroyed by the insertion of a stout needle into the spinal cord and the parts above it. One of its lower extremities is used in the following manner. The large trunk of the sciatic nerve is dissected out at the back of the thigh, and a pair of electrodes is

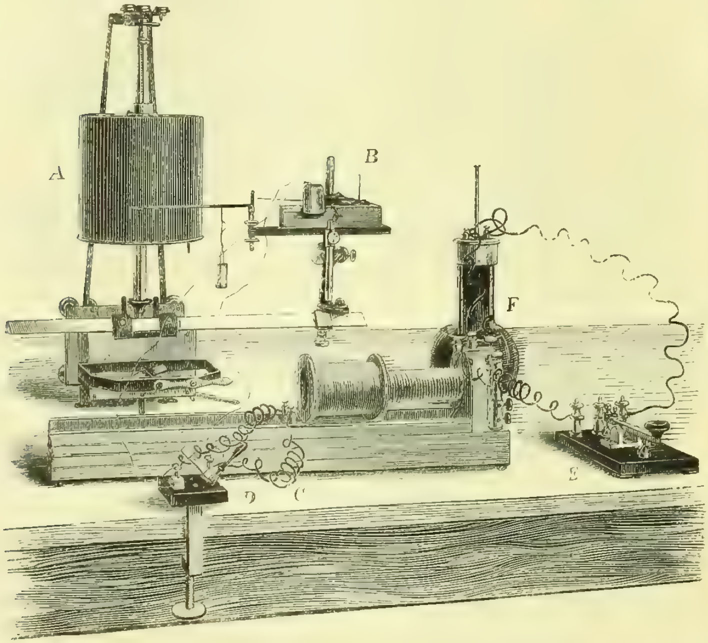


Fig. 280.—*Arrangement of the apparatus necessary for recording muscle contractions* with a revolving cylinder carrying smoked paper. A, revolving cylinder; B, the frog arranged upon a cork-covered board which is capable of being raised or lowered on the upright, which also can be moved along a solid triangular bar of metal attached to the base of the recording apparatus—the tendon of the gastrocnemius is attached to the writing lever properly weighted by a ligature. The electrodes from the secondary coil pass to the apparatus—being, for the sake of convenience, first of all brought to a key, D (Du Bois Reymond's); C, the induction coil; F, the battery (in this fig. a bichromate one); E, the key (Morse's) in the primary circuit.

inserted behind it. The tendo-achillis is divided from its attachment to the os calcis, and a ligature is tightly tied round it. This tendon is part of the broad muscle of the thigh (gastrocnemius) which arises from above the condyles of the femur. The femur is now fixed to a board covered with cork, and the ligature attached to the tendon is tied to the upright of a piece of metal bent at right angles (fig. 280, B), which is capable of movement about a pivot at its knee, the horizontal portion carrying a writing lever (myograph). When the muscle contracts the lever is raised. It is necessary to attach a small weight to the lever. In this arrangement the muscle is *in situ*, and the nerve disturbed from its relations as little as possible.

The muscle may, however, be detached from the body with the lower end of the femur from which it arises, and the nerve going to it may be taken away with it. The femur is divided at about the lower third. The bone is held in a firm clamp, the nerve is placed upon two electrodes connected with an induction apparatus, and the lower end of the muscle is connected by means of a ligature attached to its tendon with a lever which can write on a recording apparatus.

To prevent evaporation this so-called *nerve-muscle preparation* is placed under a glass shade, the air in which is kept moist by means of blotting paper saturated with saline solution.

Effect of a single Induction Shock.

Taking the nerve-muscle preparation in either of these ways, on closing or opening the key in the primary circuit we obtain and can record a contraction, and if we use the clockwork apparatus revolving rapidly, a curve is traced such as is shown in (fig. 281).

Another way of recording the contraction is by the pendulum myograph (fig. 282). Here the movement of the pendulum along a certain arc is substituted for the clockwork movement of the other apparatus. The pendulum carries a smoked glass plate upon which the writing lever of a myograph is made to mark. The opening or breaking shock is sent into the nerve-muscle preparation by the pendulum in its swing opening a key (fig. 282, *C*.) in the primary circuit.

Single Muscle Contraction.—The tracings obtained in a manner above described and seen in fig. 281, may be thus explained.

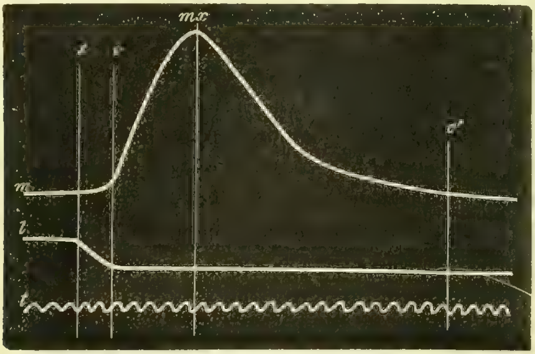


Fig. 281.—*Muscle-curve obtained by the pendulum myograph.* s, indicates the exact instant of the induction shock; *c*, commencement; and *m x*, the maximum elevation of lever; *t*, the line of a vibrating tuning-fork. (M. Foster.)

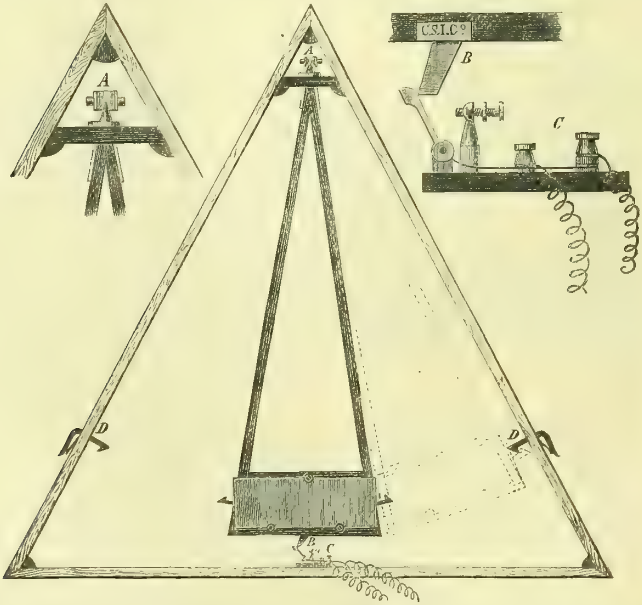


Fig. 282.—*Simple form of pendulum myograph and accessory parts.* *A*, pivot upon which pendulum swings; *B*, catch on lower end of myograph opening the key, *C*, in its swing; *D*, a spring-catch which retains myograph, as indicated by dotted lines, and on pressing down the handle of which the pendulum swings along the arc to *D* on the left of figure, and is caught by its spring.

The upper line (m) represents the curve traced by the end of the lever after stimulation of the muscle by a single induction-shock: the middle line (l) is that described by the marking-lever, and indicates by a sudden drop the exact instant at which the induction-shock was given. The lower wavy line (t) is traced by a vibrating tuning-fork, and serves to measure precisely the intervals of time occupied in each part of the contraction.

It will be observed that after the stimulus has been applied, as indicated by the vertical line s, there is an interval before the contraction commences, as indicated by the line c. This interval, termed the "*latent period*" (Helmholtz), when measured by the number of vibrations of the tuning-fork between the lines s and c, is found to be about $\frac{1}{100}$ sec.

The contraction progresses rapidly at first and afterwards more slowly to the maximum (the point in the curve through which the line mx is drawn), which takes $\frac{4}{100}$ sec., and then the muscle elongates again as indicated by the descending curve, at first rapidly, afterwards more slowly, till it attains its original length at the point indicated by the line c', occupying $\frac{5}{100}$ sec.

The muscle curve obtained from the heart resembles that of unstriped muscles in the long duration of the effect of stimulation; the descending curve is very much prolonged.

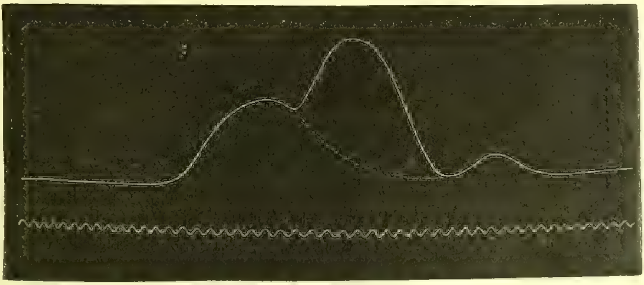


Fig. 283.—*Tracing of a double muscle-curve.* To be read from left to right. While the muscle was engaged in the first contraction (whose complete course, had nothing intervened, is indicated by the dotted line), a second induction-shock was thrown in, at such a time that the second contraction began just as the first was beginning to decline. The second curve is seen to start from the first, as does the first from the base line. (M. Foster.)

The greater part of the latent period is taken up by changes in the muscle itself, the rest being occupied in the propagation of the shock along the nerve (M. Foster).

Tetanus.—If instead of a single induction-shock through the preparation we pass two, one immediately after the other, when the point of stimulation of the second one corresponds to the maximum of the first, a second curve (fig. 283) will occur which will commence at the highest point of the first and will rise as high, so that the sum of the height of the two exactly equals twice the height of the first. If a third and a fourth shock be passed, a similar effect will ensue, and curves one above the other will be traced, the third being slightly less than the second, and the fourth than the third. If the shocks be repeated at short intervals, however, the lever after a time ceases to rise any further, and the contraction which has reached its maximum is maintained (fig. 285), and the lever marks a straight line on the recording cylinder. This condition is called *tetanus of muscle.* The condition of "an ordinary tetanic muscular movement is essentially a vibratory movement, the apparently rigid and firm muscular mass is really the subject of a whole series of vibrations, a series namely of simple spasms; it will be readily

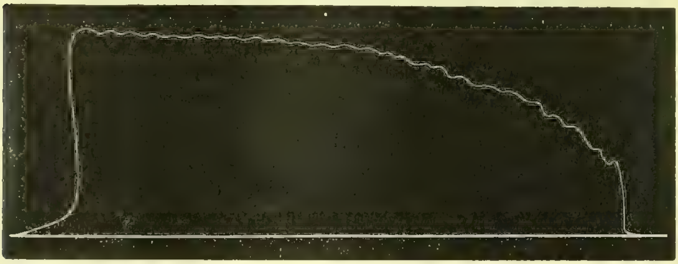


Fig. 284.—*Curve of tetanus*, obtained from the gastrocnemius of a frog, where the shocks were sent in from an induction coil, about sixteen times a second, by the interruption of the primary current by means of a vibrating spring, which dipped into a cup of mercury, and broke the primary current at each vibration.

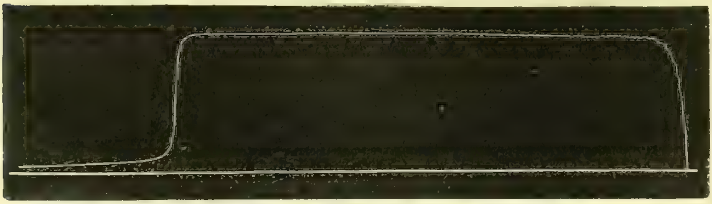


Fig. 285.—*Curve of tetanus*, from a series of very rapid shocks from a magnetic interrupter.

understood why a tetanised muscle, like all other vibrating bodies, gives out a sound" (M. Foster).

If the stimuli are not quite so rapidly sent in the line of maximum contraction becomes somewhat wavy, indicating a slight tendency of the muscle to relax during the intervals between the stimuli (fig. 284).

Muscular Work.—We have seen (p. 153) that *work* is estimated by multiplying the weight raised, by the height through which it has been lifted. It has been found that in order to obtain the maximum of work, a muscle must be moderately *loaded:* if the weight be increased beyond a certain point, the muscle becomes strained and raises the weight through so small a distance that less work is accomplished. If the load is still further increased the muscle is completely overtaxed, cannot raise the weight, and consequently does no work at all. Practical illustrations of these facts must be familiar to every one.

The power of a muscle is usually measured by the maximum weight which it will support without stretching. In man this is readily determined by weighting the body to such an extent that it can no longer be raised on tiptoe: thus the power of the calf-muscles is determined (Weber.)

The power of a muscle thus estimated depends of course upon its cross-section. The power of a human muscle is from two to three times as great as a frog's muscle of the same sectional area.

Fatigue of Muscle.—A muscle becomes rapidly exhausted from repeated stimulation, and the more rapidly, the more quickly the induction-shocks succeed each other.

This is indicated by the diminished height of contraction in the accompanying diagrams (fig. 286). It will be seen that the vertical lines, which indicate the extent of the muscular contraction, decrease in length from left to right. The line A B drawn along the tops of these lines is termed the "fatigue curve." It is usually a straight line.

In the first diagram the effects of a short rest are shown: there is a pause of three minutes, and when the muscle is again stimulated it contracts up to A′, but the recovery is only temporary, and the *fatigue curve*, after a few more contractions, becomes continuous with that before the rest.

In the second diagram is represented the effect of a stream of oxygenated blood. Here we have a sudden restoration of energy: the muscle in this case makes an entirely fresh start from A, and the new fatigue curve is parallel to, and never coincides with the old one.

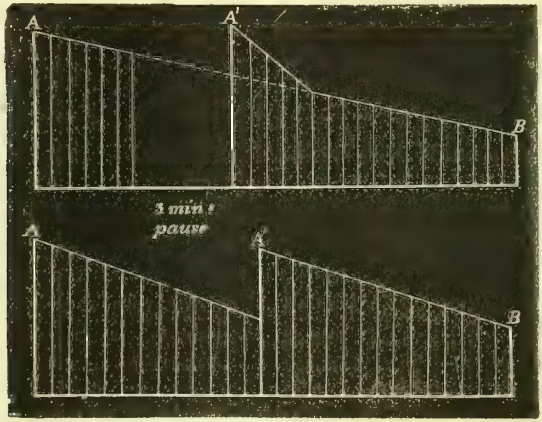


Fig. 286.—*Fatigue muscle-curves.* (Ray Lankester.)

A fatigued muscle has a much longer "latent period" than a fresh one. The slowness with which muscles respond to the will when fatigued must be familiar to every one.

In a muscle which is exhausted, stimulation only causes a contraction producing a local bulging near the point irritated. A similar effect may be produced in a fresh muscle by a sharp blow, as in striking the biceps smartly with the edge of the hand, when a hard muscular swelling is instantly formed.

Accompaniments of Muscular Contraction.—(1.) *Heat* is developed in the contraction of muscles. Becquerel and Breschet found, with the thermo-multiplier, about 1° Fahr. of heat produced by each forcible contraction of a man's biceps; and when the actions were long continued, the temperature of the muscle increased 2°. This estimate is probably high, as in the frog's muscle a considerable contraction has been found to produce an elevation of temperature equal on an average to less than $\frac{1}{5}$° C. It is not known whether this development of heat is due to chemical changes ensuing in the muscle, or to the friction of its fibres vigorously acting: in either case, we may refer to it a part of the heat developed in active exercise (p. 383).

(2.) *Sound* is said to be produced when muscles contract forcibly, as mentioned above. Wollaston showed that this sound might be easily heard by placing the tip of the little finger in the ear, and then making some muscles contract, as those of the ball of the thumb, whose sound may be conducted to the ear through the substance of the hand and finger. A low shaking or rumbling sound is heard, the height and loudness of the note being in direct proportion to the force and quickness of the muscular action, and to the number of fibres that act together, or, as it were, in time.

(3.) *Changes in shape.*—The *mode of contraction* in the transversely-striated muscular tissue has been much disputed. The most probable account is, that the contraction is effected by an approximation of the constituent parts of the fibrils, which, at the instant of contraction, without any alteration in their general direction, become closer, flatter, and wider; a condition which is rendered evident by the approximation of the transverse striæ seen on the surface of the fasciculus, and by its increased breadth and thickness. The appearance of the zigzag lines into which it was supposed the fibres are thrown in contraction, is due to the relaxation of a fibre which has been recently contracted, and is not at once stretched again by some antagonist fibre, or whose extremities are kept close together by the contractions of other fibres. The contraction is therefore a simple, and, according to Ed. Weber, an uniform, simultaneous, and steady shortening of each fibre and its contents. What each fibril or fibre loses in length, it gains in thickness: the contraction is a change of form not of size; it is, therefore, not attended with any diminution in bulk, from condensation of the tissue. This has been proved for entire muscles, by making a mass of muscle, or many fibres together, contract in a vessel full of water, with which a fine, perpendicular, graduated tube communicates. Any diminution of the bulk of the contracting muscle would be attended by a fall of fluid in the tube; but when the experiment is carefully performed, the level of the water in the tube remains the same, whether the muscle be contracted or not.

In thus shortening, muscles appear to swell up, becoming rounder, more prominent, harder, and apparently tougher. But this hardness of muscle in the state of contraction, is not due to increased firmness or condensation of the muscular tissue, but to the increased tension to which the fibres, as well as their tendons and other tissues, are subjected from the resistance ordinarily opposed to their contraction. When no resistance is offered, as when a muscle is cut off from its tendon, not only is no hardness perceived during contraction, but the muscular tissue is even softer, more extensile, and less elastic than in its ordinary uncontracted state.

(4.) *Chemical changes.*—(*a*) The reaction of the muscle which is normally alkaline or neutral becomes decidedly acid, from the development of sarcolactic acid. (*b*) The muscle gives out carbonic acid gas and takes up oxygen, the amount of the carbonic acid given out not appearing to be entirely dependent upon the oxygen taken in, and so doubtless in part arising upon some other source. (*c*) Certain imperfectly understood chemical changes occur, in all probability connected with (*a*) and (*b*). Glycogen is diminished, and muscle sugar (inosite) appears; the extractives are increased.

(5.) *Electrical changes.*—When a muscle contracts the natural muscle current or currents of rest undergo a distinct diminution, which is due to the appearance in the actively contracting muscle of currents in an opposite direction to those existing in the muscle at rest. This causes a temporary deflection of the needle of a galvanometer in a direction opposite to the original current, and is called by some the *negative variation* of the muscle current, and by others a *current of action.*

Conditions of Contraction.—(*a*) The irritability of muscle is greatest at a certain mean temperature; (*b*) after a number of contractions a muscle gradually becomes exhausted; (*c*) the activity of muscles after a time disappears altogether when they

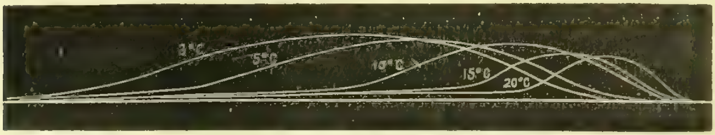


Fig. 287.—*Muscle-curves from the gastrocnemius of a frog*, illustrating effects of alterations in temperature.

are removed from the body or the arteries are tied; (*d*) oxygen is used up in muscular contraction, but a muscle will act for a time *in vacuo* or a gas which contains no oxygen: in this case it is of course using up the oxygen already in store (Hermann).

Response to Stimuli.—The two kinds of fibres, the striped and unstriped, have characteristic differences in the mode in which they act on the application of the same stimulus; differences which may be ascribed in great part to their respective differences of structure, but to some degree, possibly, to their respective modes of connection with the nervous system. When irritation is applied directly to a muscle with striated fibres, or to the motor nerve supplying it, contraction of the part irritated, and of that only, ensues; and this contraction is instantaneous, and ceases on the instant of withdrawing the irritation. But when any part with unstriped muscular fibres, *e.g.*, the intestines or bladder, is irritated, the subsequent contraction ensues more slowly, extends beyond the part irritated, and, with alternating relaxation, continues for some time after the withdrawal of the irritation. The difference in the modes of contraction of the two kinds of muscular fibres may be particularly illustrated by the effects of the electro-magnetic stimulus. The rapidly succeeding shocks given by this means to the nerves of muscles excite in all the transversely-striated muscles a fixed state of tetanic contraction as previously described, which lasts as long as the stimulus is continued, and on its withdrawal instantly ceases; but in the muscles with smooth fibres they excite, if any movement, only one that ensues slowly, is comparatively slight, alternates with rest, and continues for a time after the stimulus is withdrawn.

In their mode of responding to these stimuli, all the skeletal muscles, or those with transverse striæ, are alike; but among those with plain or unstriped fibres there are many differences,—a fact which tends to confirm the opinion that their peculiarity depends as well on their connection with nerves and ganglia as on their own properties. The ureters and gall-bladder are the parts least excited by stimuli: they do not act at all till the stimulus has been long applied, and then contract feebly, and to a small extent. The contractions of the cæcum and stomach are quicker and wider-spread: still quicker those of the iris, and of the urinary bladder if it be not too full. The actions of the small and large intestines, of the vas deferens, and pregnant uterus, are yet more vivid, more regular, and more sustained; and they require no more stimulus than that of the air to excite them. The heart, on account, doubtless, of its striated muscle, is the quickest and most vigorous of all the muscles of organic life in contracting upon irritation, and appears in this, as in nearly all other respects, to be the connecting member of the two classes of muscles.

All the muscles retain their property of contracting under the influence of stimuli applied to them or to their nerves for some time after death, the period being longer in cold-blooded than in warm-blooded Vertebrata, and shorter in Birds than in Mammalia. It would seem as if the more active the respiratory process in the living animal, the shorter is the time of duration of the irritability in the muscles after death; and this is confirmed by the comparison of different species in the same order of Vertebrata. But the period during which this irritability lasts, is not the same in all persons, nor in all the muscles of the same persons. In a man it ceases, according to Nysten, in the following order:—first in the left ventricle, then in the intestines and stomach, the urinary bladder, right ventricle, œsophagus, iris; then in the voluntary muscles of the trunk, lower and upper extremities; lastly in the right and left auricle of the heart.

III. Rigor Mortis.

After the muscles of the dead body have lost their irritability or capability of being excited to contraction by the application of a stimulus, they spontaneously pass into a state of contraction, apparently identical with that which ensues during life. It affects all the muscles of the body; and, where external circumstances do not prevent it, commonly fixes the limbs in that which is their natural posture of equilibrium or rest. Hence, and from the simultaneous contraction of all the muscles of the trunk, is produced a general stiffening of the body, constituting the *rigor mortis* or *post-mortem rigidity.*

When this condition has set in, the muscle becomes acid in reaction (due to sarco-lactic acid), and gives off carbonic acid in great excess. Its volume is slightly diminished: the muscular fibres become shortened and opaque, and their substance has set firm. It comes on much more rapidly after muscular activity, and is hastened by warmth. It may be brought on, in muscles exposed for experiment, by the action of distilled water and many acids, also by freezing and thawing again.

Cause.—The immediate cause of rigor seems coagulation of the muscle plasma (Brücke, Kühne, Norris). We may distinguish three main stages.—(1.) Gradual coagulation. (2.) Contraction of coagulated muscle-clot (myosin) and squeezing out of muscle-serum. (3.) Putrefaction. After the first stage, restoration is possible through the circulation of arterial blood through the muscles, and even when the second stage has set in, vitality may be restored by dissolving the coagulum of the muscle in salt solution, and passing arterial blood through its vessels. In the third stage recovery is impossible.

Order of Occurrence.—The muscles are not affected simultaneously by *post-mortem* contraction. It affects the neck and lower jaw first; next, the upper extremities, extending from above downwards; and lastly, reaches the lower limbs; in some rare instances only, it affects the lower extremities before, or simultaneously with, the upper extremities. It usually ceases in the order in which it began; first at the head, then in the upper extremities, and lastly in the lower extremities. It never commences earlier than ten minutes, and never later than seven hours, after death; and its duration is greater in proportion to the lateness of its accession. Heat is developed during the passage of a muscular fibre into the condition of rigor mortis.

Since rigidity does not ensue until muscles have lost the capacity of being excited by external stimuli, it follows that all circumstances which cause a speedy exhaustion of muscular irritability, induce an early occurrence of the rigidity, while conditions by which the disappearance of the irritability is delayed, are succeeded by a tardy onset of this rigidity. Hence its speedy occurrence, and equally speedy departure in the bodies of persons exhausted by chronic diseases; and its tardy onset and long continuance after sudden death from acute diseases. In some cases of sudden death from lightning, violent injuries, or paroxysms of passion, rigor mortis has been said not to occur at all; but this is not always the case. It may, indeed, be doubted whether there is really a complete absence of the post-mortem rigidity in any such cases; for the experiments of Brown-Séquard make it probable that the rigidity may supervene immediately after death, and then pass away with such rapidity as to be scarcely observable.

Experiments.—Brown-Séquard took five rabbits, and killed them by removing their hearts. In the first. rigidity came on in 10 hours, and lasted 192 hours; in the second, which was feebly electrified, it commenced in 7 hours, and lasted 144; in the third, which was more strongly electrified, it came on in two, and lasted 72 hours; in the fourth which was still more strongly electrified, it came on in one hour, and lasted 20; while, in the last rabbit, which was submitted to a powerful electro-galvanic current, the rigidity ensued in seven minutes after death, and passed away in 25 minutes. From this it appears that the more powerful the electric current, the sooner does the rigidity ensue, and the shorter is its duration; and as the lightning shock is so much more powerful than any ordinary electric discharge, the rigidity may ensue so early after death, and pass away so rapidly as to escape detection. The influence exercised upon the onset and duration of post-mortem rigidity by causes which exhaust the irritability of the muscles, was well illustrated in further experiments by the same physiologist, in which he found that the rigor mortis ensued far more rapidly, and lasted for a shorter period in those muscles which had been powerfully electrified just before death than those which had not been thus acted upon.

The occurrence of rigor mortis is not prevented by the previous existence of paralysis in a part, provided the paralysis has not been attended with very imperfect nutrition of the muscular tissue.

The rigidity affects the involuntary as well as the voluntary muscles, whether they be constructed of striped or unstriped fibres. The rigidity of involuntary muscles with striped fibres is shown in the contraction of the heart after death. The contraction of the muscles with unstriped fibres is shown by an experiment of Valentin, who found that if a graduated tube connected with a portion of intestine taken from a recently-killed animal, be filled with water, and tied at the opposite end, the water will in a few hours rise to a considerable height in the tube, owing to the contraction of the intestinal walls. It is still better shown in the arteries, of which all that have muscular coats contract after death, and thus present the roundness and cord-like feel of the arteries of a limb lately removed, or those of a body recently dead. Subsequently they relax, as do all the other muscles, and feel lax and flabby, and lie as if flattened, and with their walls nearly in contact.

Actions of the Voluntary Muscles.

The greater part of the voluntary muscles of the body act as sources of power for removing levers,—the latter consisting of the various bones to which the muscles are attached.

Examples of the three orders of levers in the Human Body.—All levers have been divided into three kinds, according to the relative position of the *power*, the *weight* to be removed, and the *axis of motion* or *fulcrum*. In a lever of the *first* kind the *power* is at one extremity of the lever, the *weight* at the other, and the *fulcrum* between the two. If the initial letters only of the *power*, *weight*, and *fulcrum* be used, the arrangement will stand thus :—P.F.W. A poker, as ordinarily used, or the bar in fig. 288 may be cited as an example of this variety of lever; while, as an instance in which the bones of the human skeleton are used as a lever of the same kind, may be mentioned the act of raising the body from the stooping posture by means of the hamstring muscles attached to the tuberosity of the ischium (fig. 288).

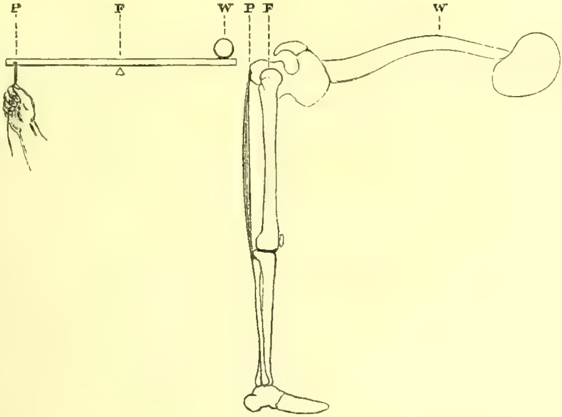


Fig. 288.

In a lever of the second kind, the arrangement is thus :—P.W.F.; and this leverage is employed in the act of raising the handles of a wheelbarrow, or in stretching an elastic band as in fig. 289. In the human body the act of opening the mouth by depressing the lower jaw is an example of the same kind,—the tension of the muscles which close the jaw representing the weight (fig. 289).

In a lever of the third kind the arrangement is—F. P. W., and the act of raising a pole, as in fig. 290, is an example. In the human body there are numerous examples of the employment of this kind of leverage. The act of bending the fore-arm may be mentioned as an instance (fig. 290). The act of biting is another example.

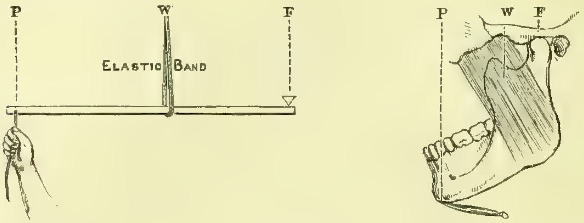


Fig. 289.

At the ankle we have examples of all three kinds of lever. 1st kind—Extending the foot. 3rd kind—Flexing the foot. In both these cases the foot represents the weight: the ankle joint the fulcrum, the power being the calf muscles in the first case, and the tibialis anticus in the second case. 2nd kind—When the body is raised on tip-toe. Here the ground is the fulcrum, the weight of the body acting at the ankle joint the weight, and the calf muscles the power.

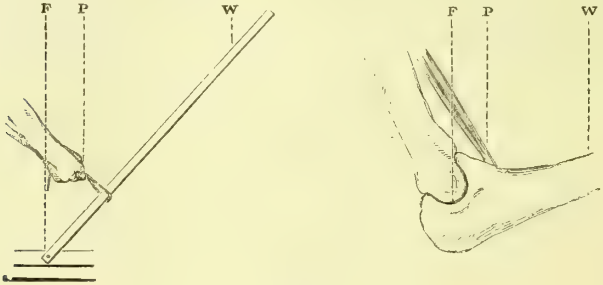


Fig. 290.

In the human body, levers are most frequently used at a disadvantage as regards power, the latter being sacrificed for the sake of a greater range of motion. Thus in the diagrams of the first and third kinds it is evident that the power is so close to the fulcrum, that great force must be exercised in order to produce motion. It is also evident, however, from the same diagrams, that by the closeness of the power to the fulcrum a great range of movement can be obtained by means of a comparatively slight shortening of the muscular fibres.

The greater number of the more important muscular actions of the human body—those, namely, which are arranged harmoniously so as to subserve some definite purpose or other in the animal economy—are described in various parts of this work, in the sections which treat of the physiology of the processes by which these muscular actions are resisted or carried out. There are, however, one or two very important and somewhat complicated muscular acts which may be best described in this place.

Walking.—In the act of walking, almost every voluntary muscle in the body is brought into play, either directly for purposes of progression, or indirectly for the proper balancing of the head and trunk. The muscles of the arms are least concerned; but even these are for the most part instinctively in action also to some extent.

Among the chief muscles engaged directly in the act of walking are those of the calf, which, by pulling up the heel, pull up also the astragalus, and with it, of course, the whole body, the weight of which is transmitted through the tibia to this bone (fig. 291). When starting to walk, say with the left leg, this raising of the body is not left entirely to the muscles of the left calf, but the trunk is thrown forward in such a way that it would fall prostrate were it not that the right foot is brought forward and planted on the ground to support it. Thus the muscles of the left calf are assisted in their action by those muscles on the front of the trunk and legs which, by their contraction, pull the body forwards; and, of course, if the trunk form a slanting line, with the inclination forwards, it is plain that when the heel is raised by the calf-muscles, the whole body will be raised, and pushed obliquely forwards and upwards. The successive acts in taking the first step in walking are represented in fig. 291, 1, 2, 3.

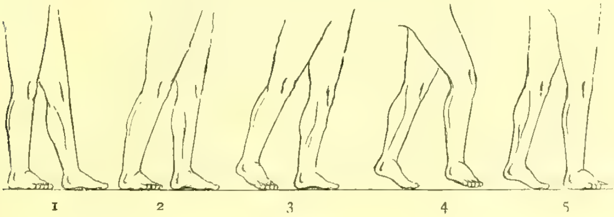


Fig. 291.

Now it is evident that by the time the body has assumed the position No. 3, it is time that the right leg should be brought forward to support it and prevent it from falling prostrate. This advance of the other leg (in this case the *right*) is effected partly by its mechanically swinging forwards, pendulum-wise, and partly by muscular action; the muscles used being,—1*st*, those on the front of the *thigh*, which bend the thigh forwards on the pelvis, especially the rectus femoris, with the psoas and the iliacus; 2*ndly*, the hamstring muscles, which slightly bend the *leg* on the thigh; and 3*rdly*, the muscles on the front of the *leg*, which raise the front of the foot and toes, and so prevent the latter in swinging forwards from hitching in the ground.

The second part of the act of walking, which has been just described, is shown in the diagram (4, fig. 291).

When the *right* foot has reached the ground the action of the *left* leg has not ceased. The calf-muscles of the latter continue to act, and by pulling up the heel, throw the body still more forwards over the *right* leg, now bearing nearly the whole weight, until it is time that in *its* turn the *left* leg should swing forwards, and the left foot be planted on the ground to prevent the body from falling prostrate. As at first, while the calf-muscles of one leg and foot are preparing, so to speak, to *push* the body forward and upward from behind by raising the heel, the muscles on the *front* of the trunk and of the same leg (and of the other leg, except when it is swinging forwards) are helping the act by *pulling* the legs and trunk, so as to make them incline forward, the rotation in the inclining forwards being effected mainly at the ankle joint. Two main kinds of leverage are, therefore, employed in the act of walking, and if this idea be firmly grasped, the detail will be understood with comparative ease. One kind of leverage employed in walking is essentially the same with that employed in pulling forward the pole, as in fig. 290. And the other, less exactly, is that employed in raising the handles of a wheelbarrow. Now, supposing the lower end of the pole to be placed in the barrow, we should have a very rough and inelegant, but not altogether bad representation of the two main levers employed in the act of walking. The body is *pulled* forward by the muscles in front, much in the same way that the pole might be by the force applied at P. (fig. 290), while the raising of the heel and *pushing* forwards of the trunk by the calf-muscles is roughly represented on raising the handles of the barrow. The manner in which these actions are performed alternately by each leg, so that one after the other is swung forwards to support the trunk, which is at the same time *pushed* and *pulled* forwards by the muscles of the other, may be gathered from the previous description.

There is one more thing to be noticed especially in the act of walking. Inasmuch as the body is being constantly supported and balanced on each leg alternately, and therefore on only one at the same moment, it is evident that there must be some provision made for throwing the centre of gravity over the line of support formed by the bones of each leg, as, in its turn, it supports the weight of the body. This may be done in various ways, and the manner in which it is effected is one element in the differences which exist in the walking of different people. Thus it may be done by an instinctive slight rotation of the pelvis on the head of each femur in turn, in such a manner that the centre of gravity of the body shall fall over the foot of this side. Thus when the body is pushed onwards and upwards by the raising, say, of the *right* heel, as in fig. 291, 3, the pelvis is instinctively by various muscles, made to rotate on the head of the left femur at the acetabulum, to the left side, so that the weight may fall over the line of support formed by the left leg at the time that the *right* leg is swinging forwards, and leaving all the work of support to fall on its fellow. Such a "rocking" movement of the trunk and pelvis, however, is accompanied by a movement of the whole trunk and leg over the foot which is being planted on the ground (fig. 292): the action being accompanied with a compensatory outward movement at the hip, more easily appreciated by looking at the figure (in which this movement is shown exaggerated) than described.

Thus the body in walking is continually rising and swaying alternately from one side to the other, as its centre of gravity has to be brought alternately over one or other leg ; and the curvatures of the spine are altered in correspondence with the varying position of the weight which it has to support. The extent to which the body is raised or swayed differs much in different people.

In walking, one foot or the other is always on the ground. The act of *leaping* or *jumping*, consists in so sudden a raising of the heels by the sharp and strong contraction of the calf-muscles, that the body is jerked off the ground. At the same time the effect is much increased by first bending the thighs on the pelvis, and the legs on the thighs, and then suddenly straightening out the angles thus formed. The share which this action has in producing the effect may be easily known by attempting to leap in the upright posture, with the legs quite straight.

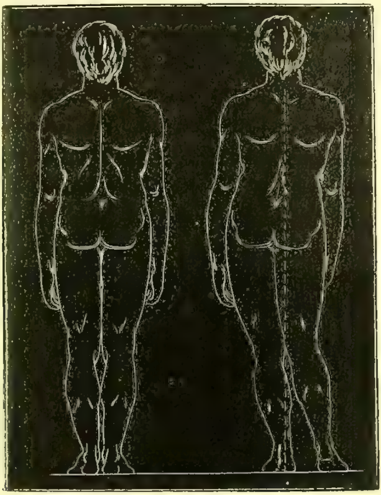


Fig. 292.

Running is performed by a series of rapid low jumps with each leg alternately ; so that, during each complete muscular act concerned, there is a moment when both feet are off the ground.

In all these cases, however, the description of the manner in which any given effect is produced, can give but a very imperfect idea of the infinite number of combined and harmoniously arranged muscular contractions which are necessary for even the simplest acts of locomotion.

Actions of the Involuntary Muscles.—The involuntary muscles are for the most part not attached to bones arranged to act as levers, but enter into the formation of such hollow parts as require a diminution of their calibre by muscular action, under particular circumstances. Examples of this action are to be found in the intestines, urinary bladder, heart and blood-vessels, gall-bladder, gland-ducts, etc.

The difference in the manner of contraction of the striated and non-striated fibres has been already referred to (p. 503); and the peculiar vermicular or peristaltic action of the latter fibres has been described at p. 503.

Source of Muscular Action.

It was formerly supposed that each act of contraction on the part of a muscle was accompanied by a correlative waste or destruction of its own substance; and that the quantity of the nitrogenous excreta, especially of urea, presumably the expression of this waste, was in exact proportion to the amount of muscular work performed. It has been found, however, both that the theory itself is erroneous, and that the supposed facts on which it was founded do not exist.

It is true that in the action of muscles, as of all other parts, there is a certain destruction of tissue or, in other words, a certain 'wear and tear,' which may be represented by a slight increase in the quantity of urea excreted: but it is not the *correlative* expression or *only* source of the power manifested. The increase in the amount of urea which is excreted after muscular exertion is by no means so great as was formerly supposed; indeed, it is very slight. And as there is no reason to believe that the waste of muscle-substance can be expressed, with unimportant exceptions, in any other way than by an increased excretion of urea, it is evident that we must look elsewhere than in destruction of muscle, for the source of muscular action. For, it need scarcely be said, all force manifested in the living body must be the correlative expression of force previously latent in the food eaten or the tissue formed; and evidences of force expended in the body must be found in the *excreta*. If, therefore, the *nitrogenous* excreta, represented chiefly by urea, are not in sufficient quantity to account for the work done, we must look to the *non-nitrogenous* excreta as carbonic acid and water, which, presumably, cannot be the expression of wasted muscle-substance.

The quantity of these non-nitrogenous excreta is undoubtedly increased by active muscular efforts, and to a considerable extent;

and whatever may be the source of the water, the carbonic acid, at least, is the result of chemical action in the system, and especially of the combustion of non-nitrogenous food, although, doubtless, of nitrogenous food also. We are, therefore, driven to the conclusion,—that the substance of muscles is not wasted in proportion to the work they perform; and that the non-nitrogenous as well as the nitrogenous foods may, in their combustion, afford the requisite conditions for muscular action. The urgent necessity for *nitrogenous* food, especially after exercise, is probably due more to the need of *nutrition* by the exhausted muscles and other tissues for which, of course, nitrogen is essential, than to such food being superior to *non-nitrogenous* substances as a source of muscular power.

The electrical condition of Nerves is so closely connected with the phenomena of muscular contraction, that it will be convenient to consider it in the present chapter.

Electrical currents in Nerves—If a piece of nerve be removed from the body and subjected to examination in a way similar to that adopted in the case of muscle which has been described (p. 485), electrical currents are found to exist which correspond exactly to the natural muscle currents, and which are called *natural nerve currents* or *currents of rest*, according as one or other theory of their existence be adopted, as in the case with muscle. One point (corresponding to the equator) on the surface being positive to all other points nearer to the cut ends, and the greatest deflection of the needle of the galvanometer taking place when one electrode is applied to the equator and the other to the centre of either cut end. As in the case of muscle, these nerve-currents undergo a *negative variation* when the nerve is stimulated, the variation being momentary and in the opposite direction to the natural currents; and are similarly known as the *currents of action*. The currents of action are propagated in both directions from the point of the application of the stimulus, and are of momentary duration.

Rheoscopic Frog.—The negative variation of the nerve current may be demonstrated by means of the following experiment.—The new current produced by stimulating the nerve of one nerve-muscle preparation may be used to stimulate the nerve of a second nerve-muscle preparation. The foreleg of a frog with the nerve going to the gastrocnemius cut long is placed upon a glass plate, and arranged in such a way that its nerve touches in two places the sciatic nerve, exposed but preserved *in situ* in the thigh of the opposite leg. The electrodes from an induction coil are placed behind the sciatic nerve of the second preparation, high up. On stimulating the nerve with a single induction shock, the muscles not only of the same leg are found to undergo a twitch, but also those of the first preparation, although this is not near the electrodes, and so the stimulation cannot be due to an escape of the current into the first nerve. This experiment is known under the name of the *rheoscopic frog.*

Nerve-stimuli.—Nerve-fibres require to be stimulated before they can manifest any of their properties, since they have no power of themselves of generating force or of originating impulses. The stimuli which are capable of exciting nerves to action, are, as in the case of muscle, very diverse. They are of very similar nature in each case. The mechanical, chemical, thermal, and electric stimuli which may be used in the one case are also, with certain differences in the methods employed, efficacious in the other. The chemical stimuli are chiefly these: withdrawal of water, as by drying, strong solutions of neutral salts of potassium, sodium, &c., free inorganic acids, except phosphoric; some organic acids; ether, chloroform, and bile salts. The electrical stimuli employed are the induction and continuous currents concerning which the observations in reference to muscular contraction should be consulted p. 491 *et seq.* Weaker electrical stimuli will excite nerve than will excite muscle; the nerve stimulus appears to gain strength as it descends, and a weaker stimulus applied far from the muscle will have the same effect as a somewhat stronger one applied to the nerve near the muscle.

It will be only necessary here to add some account of the effect of a constant electrical current, such as that obtained from Daniell's battery, upon a nerve. This effect may be studied with the apparatus described before. A pair of electrodes are placed behind the nerve of the nerve-muscle preparation, with a Du Bois Reymond's key arranged for short circuiting the battery current, in such a way that when the key is opened the current is sent into the nerve, and when closed the current is cut off. It will be found that with a current of moderate strength there will be a contraction of the muscle both at the opening and at the closing of the key (called respectively *making* and *breaking* contractions), but that during the interval between these two events the muscle remains flaccid, provided the battery current continues of constant intensity. If the current be a very weak or a very strong one the effect is not quite the same; one or other of the contractions may be absent. Which of these contractions is absent depends upon another circumstance, viz., the direction of the current. The direction of the current may be *ascending* or *descending;* if ascending, the anode or positive pole is nearer the muscle than the kathode or negative pole, and the current to return to the battery has to pass up the nerve, if descending, the position of the electrodes is reversed. It will be necessary before considering this question further to return to the want of apparent effect of the constant current during the interval between the make and break contraction: to all appearance, indeed, no effect is produced at all, but in reality a very important change is brought about in the nerve by the passage of the current. This may be shown in two ways, first of all by the galvanometer. If a piece of nerve be taken, and if at either end an arrangement be made to test the electrical condition of the nerve by means of a pair of non-polarisable electrodes connected with a galvanometer, while to the central portion a pair of electrodes connected with a Daniell's battery be applied, it will be found that the natural nerve-currents are profoundly altered on the passage of the constant current (which is called the polarising current) in the neighbourhood. If the polarising current be in the same direction as the latter the natural current is increased, but if in the direction opposite to it, the natural current is diminished. This change, produced by the continual passage of the battery-current through a portion of the nerve is to be distinguished from the negative variation of the natural current to which allusion has been already made, and which is a momentary change occurring on the sudden application of the stimulus. The condition produced in a nerve by the passage of a constant current is known by the name of *electrotonus.*

The other way of showing the effect of the same polarising current is by taking a nerve-muscle preparation and applying to the nerve a pair of electrodes from an induction coil whilst at a point further removed from the muscle, electrodes from a Daniell's battery are arranged with a key for short circuiting and an apparatus (reverser) by which the battery current may be reversed in direction. If the exact point be ascertained to which the secondary coil should be moved from the primary coil in order that a minimum contraction be obtained by the induction shock, and the secondary coil be removed slightly further from the primary, the induction current cannot now produce a contraction ; but if the polarising current be sent in a descending direction, that is to say, with the kathode nearest the other electrodes, the induction current, which was before insufficient, will prove sufficient to cause a contraction ; whereby indicating that with a descending current the irritability of the nerve is increased. By means of a somewhat similar experiment it may be shown that an ascending current will diminish the irritability of a nerve. Similarly, if instead of applying the induction electrodes below the other electrodes they are applied between them, like effects are demonstrated, indicating that in the neighbourhood of the kathode the irritability of the nerve is increased by a constant current, and in the neighbourhood of the anode diminished. This increase in irritability is called *katelectrotonus*, and similarly the decrease is called *anelectrotonus*. As there is between the electrodes both an increase and a decrease of irritability on the passage of a polarising current it must be evident that the increase must shade off into the decrease, and that there must be a neutral point where there is neither increase nor decrease of irritability. The position of this

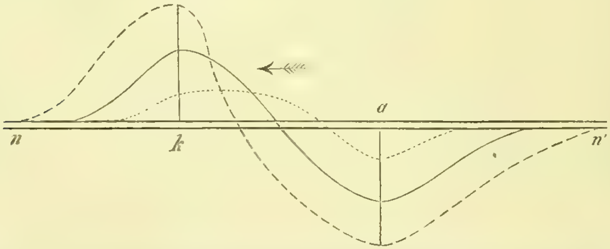


Fig. 293.—*Diagram illustrating the effects of various intensities of the polarising currents.* *n*, *n'* nerve ; *a*, anode ; *k*, kathode ; the curves above indicate increase, and those below decrease of irritability, and when the current is small the increase and decrease are both small, with the neutral point near *a*, and so on as the current is increased in strength.

neutral point is found to vary with the intensity of the polarising current, when the current is weak the point is nearer the anode, when strong nearer the kathode (fig. 293). When a constant current passes into a nerve, therefore, if a making contraction result, it may be assumed that it is due to the increased irritability produced in the neighbourhood of the kathode, but the breaking contraction must be produced by a rise in irritability from a lowered state to the normal in the neighbourhood of the anode. The contractions produced in the muscle of a nerve-muscle preparation by a constant current have been arranged in a table which is known as Pflüger's Law of Contractions. It is really only a statement as to when a contraction may be expected :—

	DESCENDING CURRENT.		ASCENDING CURRENT.	
	Make.	Break.	Make.	Break.
Weak	Yes.	No.	Yes.	No.
Moderate ...	Yes.	Yes.	Yes.	Yes.
Strong	Yes.	No.	No.	Yes.

The difficulty in this table is chiefly in the effect of a weak current, but the following statement will explain it. The increase of irritability at the kathode is more potent to produce a contraction than the rise of irritability from a lower to a normal condition at the anode. With weak currents the only effect is a contraction at the make of both ascending and descending currents, the descending current being more potent than the ascending (and with still weaker currents is the only one which produces any effect), since the kathode is near the muscle, whereas in the case of the ascending current the stimulus has to pass through a district of diminished irritability, which may either act as an entire block, or may diminish slightly the contraction which follows. As the polarising current becomes stronger, recovery from anelectrotonus is able to produce a contraction as well as katelectrotonus, and a contraction occurs both at the make and the break of the current. The absence of contraction with a very strong current at the break of the ascending current may be explained by supposing that the region of fall in irritability at the kathode blocks the stimulus of the rise in irritability at the anode.

Thus we have seen that two circumstances influence the effect of the constant current upon a nerve, viz., the strength and direction of the current. It is also necessary that the stimulus should be applied suddenly and not gradually, and that the irritability of the nerve be normal, and not increased or diminished. Sometimes (when the nerve is specially irritable?) instead of a simple contraction a tetanus occurs at the make or break of the constant current. This is especially liable to occur at the break of a strong ascending current which has been passing for some time into the preparation ; this is called *Ritter's tetanus*, and may be increased by passing a current in an opposite direction or stopped by passing a current in the same direction.

CHAPTER XVI.

THE VOICE AND SPEECH.

In nearly all air-breathing vertebrate animals there are arrangements for the production of sound, or *voice*, in some parts of the respiratory apparatus. In many animals, the sound admits of being variously modified and altered during and after its production ; and, in man, one such modification occurring in obedience to dictates of the cerebrum, is *speech*.

Mode of Production of the Human Voice.

It has been proved by observations on living subjects, by means of the laryngoscope, as well as by experiments on the larynx taken from the dead body, that the sound of the human voice is the result of the inferior laryngeal ligaments, or true vocal cords (A, *cv*, fig. 298) which bound the *glottis*, being thrown into vibration by currents of expired air impelled over their edges. Thus, if a free opening exists in the trachea, the sound of the voice ceases, but returns if the opening is closed. An opening into the air-passages above the glottis, on the contrary, does not prevent the voice being formed. Injury of the laryngeal nerves supplying the muscles which move the vocal cords puts an end to the formation of vocal sounds; and when these nerves are divided on both sides, the loss of voice is complete. Moreover, by forcing a current of air through the larynx in the dead subject, clear vocal sounds are produced, though the epiglottis, the upper ligaments of the larynx or false vocal cords, the ventricles between them and the inferior ligaments or true vocal cords, and the upper part of the arytenoid cartilages, be all removed; provided the true vocal cords remain entire, with their points of attachment, and be kept tense and so approximated that the fissure of the glottis may be narrow.

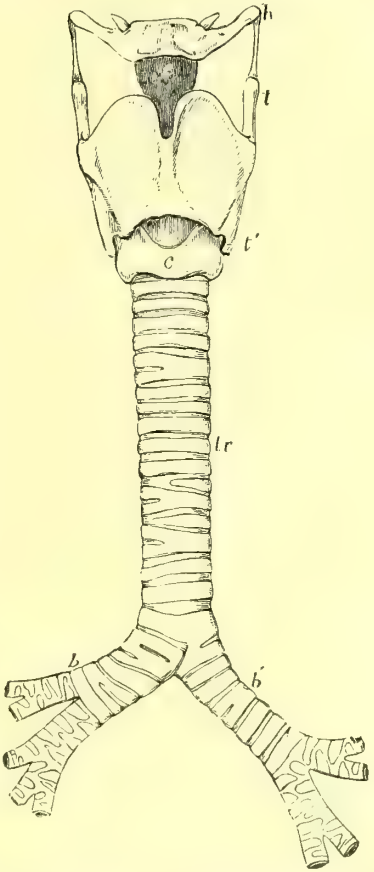


Fig. 294.—*Outline showing the general form of the larynx, trachea, and bronchi, as seen from before.* *h*, the great cornu of the hyoid bone; *e*, epiglottis; *t*, superior, and *t'*, inferior cornu of the thyroid cartilage; *c*, middle of the cricoid cartilage; *tr*, the trachea, showing sixteen cartilaginous rings; *b*, the right, and *b'*, the left bronchus. × ½. (Allen Thomson.)

The vocal ligaments or cords, therefore, may be regarded as the proper organs of the mere voice: the modifications of the voice being effected by other parts—tongue, teeth, lips, etc., as well as by them. The structure of the vocal cords is adapted to enable them to vibrate like tense membranes, for they are essentially composed of elastic tissue; and they are so attached to the cartilaginous parts of the larynx that their position and tension can be variously altered by the contraction of the muscles which act on these parts.

The Larynx.—The *larynx*, or organ of voice, consists essentially of the two vocal cords, which are so attached to certain cartilages, and so under the control of certain muscles, that they can be made the means not only of closing the aperture of the larynx (rima glottidis), of which they are the lateral boundaries, against the entrance and exit of air to or from the lungs, but also can be stretched or relaxed, shortened or lengthened, in accordance with the conditions that may be necessary for the air in passing over them, to set them vibrating and produce various sounds. Their action in respiration has been already referred to (p. 234). In the present chapter the sound produced by the vibration of the vocal cords is the only part of their function with which we have to deal.

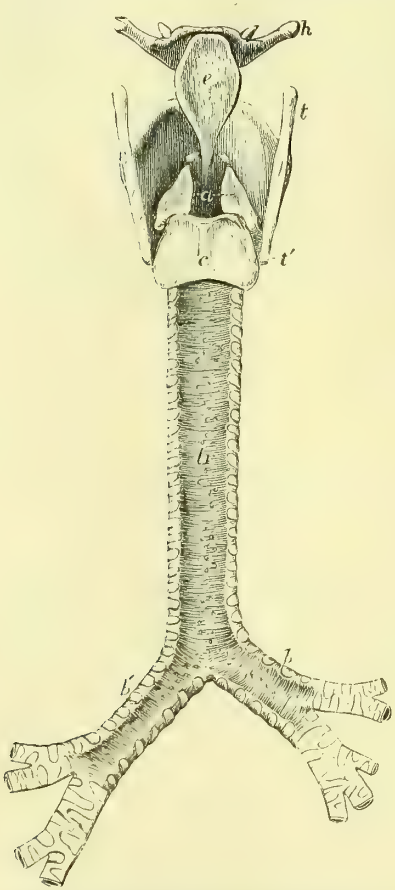


Fig. 295.—*Outline showing the general form of the larynx, trachea, and bronchi, as seen from behind.* *h*, great cornu of the hyoid bone; *t*, superior, and *t′*, the inferior cornu of the thyroid cartilage; *e*, the epiglottis; *a*, points to the back of both the arytenoid cartilages, which are surmounted by the cornicula; *c*, the middle ridge on the back of the cricoid cartilage; *t r*, the posterior membranous part of the trachea; *b*, *b′*, right and left bronchi. × ½. (Allen Thomson.)

Anatomy of the Larynx—The principal parts entering into the formation of the larynx (figs. 294 and 295) are—(*t*) the thyroid cartilage; (*c*) the cricoid cartilage; (*a*) the two arytenoid cartilages; and the two true vocal cords (A, *cv*, fig. 298). The epiglottis (fig. 298 *e*), has but little to do with the voice, and is chiefly useful in falling down as a "lid" over the upper part of the larynx, to help in preventing the entrance of food and drink in deglutition. It also guides mucus or other fluids in small amount from the mouth around the sides of the upper opening of the glottis into the pharynx and œsophagus: thus preventing them from entering the larynx. The false vocal cords (*cvs*, fig. 298), and the ventricle of the larynx, which is a space between the false and the true cord of either side, need be here only referred to.

Cartilages.—The thyroid cartilage (fig. 296, 1 to 4) does not form a complete ring around the larynx, but only covers the front portion. The cricoid cartilage (fig. 296, 5, 6), on the other hand, is a complete ring; the back part of the ring being much broader than the front. On the top of this broad portion of the cricoid are the arytenoid cartilages (fig. 298 *a*) the connection between the crioid below and arytenoid cartilages above being a joint with synovial membrane and ligaments, the latter permitting tolerably free motion between them. But although the arytenoid cartilages can move on the cricoid, they of course accompany the latter in all their movements, just as the head may nod or turn on the top of the spinal column, but must accompany it in all its movements as a whole.

Ligaments.—The thyroid cartilage is also connected with the cricoid, not only by ligaments, but by two joints with synovial membrane (t′, figs. 294 and 295); the lower *cornua* of the thyroid clasping, or nipping, as it were, the cricoid between them, but not so tightly but that the thyroid can revolve, within a certain range, around an axis passing transversely through the two joints at which the cricoid is clasped. The vocal cords are attached (behind) to the front portion of the base of the arytenoid cartilages, and (in front) to the re-entering angle at the back part of the thyroid; it is evident, therefore, that all movements of either of these cartilages must produce an effect on them of some kind or other. Inasmuch, too, as the arytenoid cartilages rest on the top of the back portion of the cricoid cartilage (*a*, fig. 298), and are connected with it by capsular and other ligaments, all movements of the cricoid cartilage must move the arytenoid cartilages, and also produce an effect on the vocal cords.

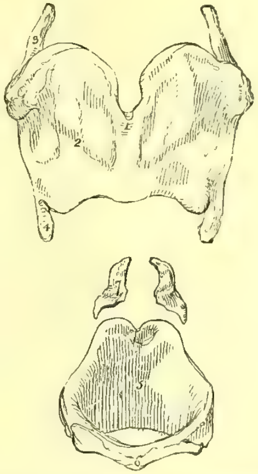


Fig. 296.—*Cartilages of the larynx seen from before.* 1 to 4, thyroid cartilage; 1, vertical ridge or pomum Adami; 2, right ala; 3, superior, and 4, inferior cornu of the right side; 5, 6, cricoid cartilage; 5, inside of the posterior part; 6, anterior narrow part of the ring; 7, arytenoid cartilages. $\times \frac{3}{4}$.

Intrinsic Muscles.—The so-called *intrinsic* muscles of the larynx, or those which, in their action, have a direct action on the vocal cords, are nine in number—four pairs, and a single muscle; namely, two *crico-thyroid* muscles, two *thyro-arytenoid*, two *posterior crico-arytenoid*, two *lateral crico-arytenoid*, and one *arytenoid* muscle. Their actions are as follows:—When the *crico-thyroid* muscles (10, fig. 297) contract, they rotate the cricoid on the thyroid cartilage in such a manner that the upper and back part of the former, and of necessity the arytenoid cartilages on the top of it, are tipped backwards, while the thyroid is inclined forward: and thus, of course, the vocal cords being attached in front to one, and behind to the other, are "put on the stretch."

The *thyro-arytenoid* muscles (7. fig. 300) on the other hand, have an opposite action,—pulling the *thyroid* backwards, and the *arytenoid* and upper and back part of the *cricoid* cartilages forwards, and thus *relaxing* the vocal cords.

The *crico-arytenoidei postici* muscles (fig. 299, *b*) *dilate* the glottis, and separate the vocal cords, the one from the other, by an action on the arytenoid cartilage which will be plain on reference to B′ and C′, (fig. 298). By their contraction they tend to *pull together* the outer angles of the arytenoid cartilages in such a fashion as to rotate the latter at their joint with the cricoid, and of course to throw asunder their anterior angles to which the vocal cords are attached.

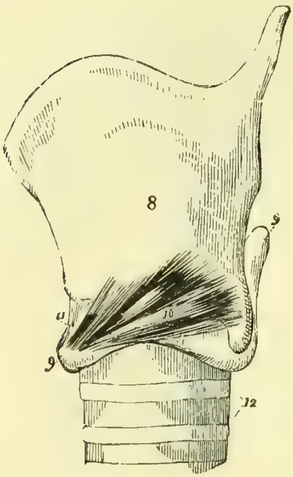


Fig. 297.—*Lateral view of exterior of the larynx.* 8, thyroid cartilage; 9, cricoid cartilage; 10, crico-thyroid muscle; 11, crico-thyroid ligament; 12, first rings of trachea. (Willis.)

These *posterior* crico-arytenoid muscles are opposed by the *cryco-arytenoidei laterales,* which, pulling in the opposite direction from the other side of the axis of rotation, have of course exactly the opposite effect, and close the glottis (fig. 300, 4 and 5).

The aperture of the glottis can be also contracted by the *arytenoid* muscle (*s*, fig. 299 and 6, fig. 300), which, in its contraction, pulls together the upper parts of the arytenoid cartilages between which it extends.

Nerve Supply.—In the performance of the functions of the larynx the sensory filaments of the pneumogastric supply that acute sensibility by which the glottis is guarded against the ingress of foreign bodies, or of irrespirable gases. The contact of these stimulates the filaments of the superior laryngeal branch of the pneumogastric; and the impression conveyed to the medulla oblongata, whether it produce sensation or not, is reflected to the filaments of the recurrent or inferior laryngeal branch, and excites contraction of the muscles that close the glottis. Both these branches of pneumogastric co-operate also in the production and regulation of the voice; the inferior laryngeal determining the contraction of the muscles that vary the tension of the vocal cords, and the superior laryngeal conveying to the mind the sensation of the state of these muscles necessary for their continuous guidance. And both the branches co-operate in the actions of the larynx in the ordinary slight dilatation and contraction of the glottis in the acts of expiration and inspiration, and more evidently in those of coughing and other forcible respiratory movements.

Movements of Vocal Cords.—The placing of the vocal cords in a position parallel one with the other, is effected by a combined action of the various little muscles which act on them —the thyro-arytenoidei having, without much reason, the credit of taking the largest share in the production of this effect. Fig. 298 is intended to show the various positions of the vocal cord under different circumstances. Thus, in ordinary tranquil breathing, the opening of the glottis is wide and triangular (B) becoming a little wider at each inspiration, and a little narrower at each expiration. On making a rapid and deep inspiration the opening of the glottis is widely dilated (as in C), and somewhat lozenge-shaped. At the moment of the emission of sound, it is narrowed,

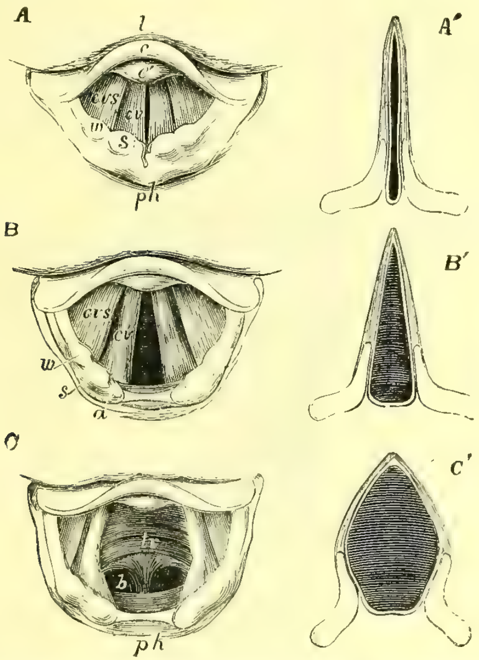


Fig. 298.—*Three laryngoscopic views of the superior aperture of the larynx and surrounding parts.* A, the glottis during the emission of a high note in singing; B, in easy and quiet inhalation of air; C, in the state of widest possible dilatation, as in inhaling a very deep breath. The diagrams A′, B′, and C′, have been added to Czermak's figures, to show in horizontal sections of the glottis the position of the vocal ligaments and arytenoid cartilages in the three several states represented in the other figures. In all the figures, so far as marked, the letters indicate the parts as follows, viz.: *l*, the base of the tongue; *e*, the upper free part of the epiglottis; *e′*, the tubercle or cushion of the epiglottis; *ph*, part of the anterior wall of the pharynx behind the larynx; in the margin of the aryteno-epiglottidean fold *w*, the swelling of the membrane caused by the cartilages of Wrisberg; *s*, that of the cartilages of Santorini; *a*, the tip or summit of the arytenoid cartilages; *c v*, the true vocal cords or lips of the rima glottidis; *c v s*, the superior or false vocal cords; between them the ventricle of the larynx; in C, *tr* is placed on the anterior wall of the receding trachea, and *b* indicates the commencement of the two bronchi beyond the bifurcation which may be brought into view in this state of extreme dilatation. (Czermak.) (From Quain's Anatomy.)

the margins of the arytenoid cartilages being brought into contact and the edges of the vocal cords approximated and made parallel, at the same time that their tension is much increased. The higher the note produced, the tenser do the cords become (fig. 298, A); and the range of a voice depends, of course, in the main, on the extent to which the degree of tension of the vocal cords can be thus altered. In the production of a high note, the vocal cords are brought well within sight, so as to be plainly visible with the help of the laryngoscope. In the utterance of grave tones, on the other hand, the epiglottis is depressed and brought over them, and the arytenoid cartilages look as if they were trying to hide themselves under it (fig. 301). The *epiglottis*, by being somewhat pressed down so as to cover the superior cavity of the larynx, serves to render the notes deeper in tone, and at the same

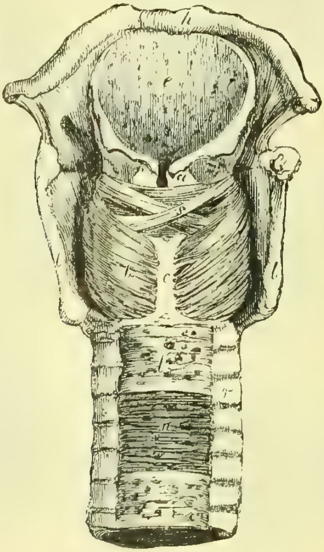


Fig. 299.—*View of the larynx and part of the trachea from behind*, with the muscles dissected; *h*, the body of the hyoid bone; *e*, epiglottis: *t*, the posterior borders of the thyroid cartilage: *c*, the median ridge of the cricoid; *a*, upper part of the arytenoid; *s*, placed on one of the oblique fasciculi of the arytenoid muscle; *b*, left posterior crico-arytenoid muscle; ends of the incomplete cartilaginous rings of the trachea; *l*, fibrous membrane crossing the back of the trachea; *n*, muscular fibres exposed in a part (from Quain's Anatomy).

time somewhat duller, just as covering the end of a short tube placed in front of caoutchouc tongues lowers the tone. In no other respect does the epiglottis appear to have any effect in modifying the vocal sounds.

The degree of approximation of the vocal cords also usually corresponds with the height of the note produced; but probably not always, for the width of the aperture has no essential influence on the height of the note, as long as the vocal cords have the same tension: only with a wide aperture, the tone is more difficult to produce, and is less perfect, the rushing of the air through the aperture being heard at the same time.

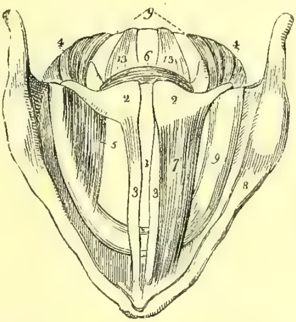


Fig. 300.—*View of the anterior of larynx from above.* 1, aperture of glottis; 2, arytenoid cartilages; 3, vocal cords; 4, posterior crico-arytenoid muscles; 5, lateral crico-arytenoid muscle of right side, that of left side removed 6, arytenoid muscle; 7, thyro-arytenoid muscle of left side, that of right side removed; 8, thyroid cartilage; 9, cricoid cartilage; 13, posterior crico-arytenoid ligament. (Willis.)

No true vocal sound is produced at the posterior part of the aperture of the glottis, that, viz., which is formed by the space between the arytenoid cartilages. For, as Müller's experiments showed, if the arytenoid cartilages be approximated in such a manner that their anterior processes touch each other, but yet leave an opening behind them as well as in front, no second vocal tone is produced by the passage of the air through the posterior opening, but merely a rustling or bubbling sound; and the height or pitch of the note produced is the same whether the posterior part of the glottis be open or not, provided the vocal cords maintain the same degree of tension.

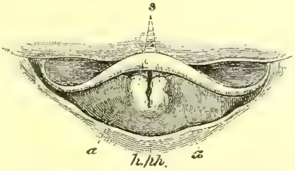


Fig. 301.—*View of the upper part of the larynx* as seen by means of the laryngoscope during the utterance of a grave note. *c*, epiglottis; *s*, tubercles of the cartilages of Santorini; *a*, arytenoid cartilages; *z*, base of the tongue; *hph*, the posterior wall of the pharynx (Czermak).

Application of the Voice in Singing and Speaking.

Varieties of Vocal Sounds.—The notes of the voice thus produced may observe three different kinds of sequence. *The first* is the monotonous, in which the notes have nearly all the same pitch as in ordinary speaking; the variety of the sounds of speech being due to articulation in the mouth. In speaking, however, occasional syllables generally receive a higher intonation for the sake of accent. *The second mode* of sequence is the successive transition from high to low notes, and *vice versâ*, without intervals; such as is heard in the sounds, which, as expressions of passion, accompany crying in men, and in the howling and whining of dogs. *The third mode* of sequence of the vocal sounds is the musical, in which each sound has a determinate number of vibrations, and the numbers of the vibrations in the successive sounds have the same relative proportions that characterise the notes of the musical scale.

Compass of the Voice.—In different individuals this comprehends one, two, or three octaves. In singers—that is, in persons apt for singing—it extends to two or three octaves. But the male and female voices commence and end at different points of the musical scale. The lowest note of the female voice is about an octave higher than the lowest of the male voice; the highest note of the female voice about an octave higher than the highest of the male. The compass of the male and female voices taken together, or the entire scale of the human voice, includes about four octaves. The principal difference between the male and female voice is, therefore, in their *pitch;* but they are also distinguished by their *tone*,—the male voice is not so soft.

Pitch and Timbre.—The voice presents other varieties besides that of male and female; there are two kinds of male voice, technically called the bass and tenor, and two kinds of female voice, the contralto and soprano, all differing from each other in tone. The bass voice usually reaches lower than the tenor, and its strength lies in the low notes; while the tenor voice extends higher than the bass. The contralto voice has generally lower notes than the soprano, and is strongest in the lower notes of the female voice; while the soprano voice reaches higher in the scale. But the difference of compass, and of power in different parts of the scale, is not the essential distinction between the different voices; for bass singers can sometimes go very high, and the contralto frequently sings the high notes like soprano singers. The essential difference between the bass and tenor voices, and between the contralto and soprano, consists in their tone or "timbre," which distinguishes them even when they are singing the same note. The qualities of the barytone and mezzo-soprano voices are less marked; the barytone being intermediate, between the bass and tenor, the mezzo-soprano between the contralto and soprano. They have also a middle position as to pitch in the scale of the male and female voices.

The different pitch of the male and the female voices depends on the different length of the vocal cords in the two sexes; their relative length in men and women being as three to two. The difference of the two voices in tone or "timbre," is owing to the different nature and form of the resounding walls, which in the male larynx are much more extensive, and form a more acute angle anteriorly. The different qualities of the tenor and bass, and of the alto and soprano voices, probably depend on some peculiarities of the ligaments, and the membranous and cartilaginous parietes of the laryngeal cavity, which are not at present understood, but of which we may form some idea, by recollecting that musical instruments made of different materials, *e.g.*, metallic and gut-strings, may be tuned to the same note, but that each will give it with a peculiar tone or "timbre."

Varieties of Voices.—The larynx of boys resembles the female larynx; their vocal cords before puberty have not two-thirds the length which they acquire at that period; and the angle of their thyroid cartilage is as little prominent as in the female larynx. Boys' voices are alto and soprano, resembling in pitch those of women, but louder, and differing somewhat from them in tone. But, after the larynx has undergone the change produced during the period of development at puberty, the boy's voice becomes bass or tenor. While the change of form is taking place, the voice is said to "crack;" it becomes imperfect, frequently hoarse and crowing, and is unfitted for singing until the new tones are brought under command by practice. In eunuchs, who have been deprived of the testes before puberty, the voice does not undergo this change. The voice of most old people is deficient in tone, unsteady, and more restricted in extent: the first defect is owing to the ossification of the cartilages of the larynx and the altered condition of the vocal cord; the want of steadiness arises from the loss of nervous power and command over the muscles; the result of which is here, as in other parts, a tremulous motion. These two causes combined render the voices of old people void of tone, unsteady, bleating, and weak.

In any class of persons arranged, as in an orchestra, according to the character of voices, each would possess, with the general characteristics of a bass, or tenor, or any other kind of voice, some peculiar character by which his voice would be recognised from all the rest. The conditions that determine these distinctions are, however, quite unknown. They are probably inherent in the tissues of the larynx, and are as indiscernible as the minute differences that characterise men's features; one often observes, in like manner, hereditary and family peculiarities of voice, as well marked as those of the limbs or face.

Most persons, particularly men, have the power, if at all capable of singing, of modulating their voices through a double series of notes of different character: namely, the notes of the natural voice, or *chest-notes*, and the *falsetto notes*. The natural voice, which alone has been hitherto considered, is fuller, and excites a distinct sensation of much stronger vibration and resonance than the falsetto voice, which has more a flute-like character. The deeper notes of the male voice can be produced only with the natural voice, the highest with the falsetto only; the notes of middle pitch can be produced either with the natural or falsetto voice; the two registers of the voice are therefore not limited in such a manner as that one ends when the other begins, but they run in part side by side.

Method of the Production of Notes.—The natural or chest-notes, are produced by the ordinary vibrations of the vocal cords. The mode of production of the falsetto notes is still obscure.

By Müller the falsetto notes were thought to be due to vibrations of only the inner borders of the vocal cords. In the opinion of Petrequin and Diday, they do not result from vibrations of the vocal cords at all, but from vibrations of the air passing through the aperture of the glottis, which they believe assumes, at such times, the contour of the *embouchure* of a flute. Others (considering some degree of similarity which exists between the falsetto notes and the peculiar tones called harmonic, which are produced when, by touching or stopping a harp-string at a particular point, only a portion of its length is allowed to vibrate) have supposed that, in the falsetto notes, portions of the vocal ligaments are thus isolated, and made to vibrate while the rest are held still. The question cannot yet be settled; but any one in the habit of singing may assure himself, both by the difficulty of passing smoothly from one set of notes to the other, and by the necessity of exercising himself in both registers, lest he should become very deficient in one, that there must be some great difference in the modes in which their respective notes are produced.

The strength of the voice depends partly on the degree to which the vocal cords can be made to vibrate; and partly on the fitness for resonance of the membranes and cartilages of the larynx, of the parietes of the thorax, lungs, and cavities of the mouth, nostrils, and communicating sinuses. It is diminished by anything which interferes with such capability of vibration. The intensity or loudness of a given note with maintenance of the same "pitch," cannot be rendered greater by merely increasing the force of the current of air through the glottis; for increase of the force of the current of air, *cæteris paribus*, raises the pitch both of the natural and the falsetto notes. Yet, since a singer possesses the power of increasing the loudness of a note from the faintest "piano" to "fortissimo" without its pitch being altered, there must be some means of compensating the tendency of the vocal cords to emit a higher note when the force of the current of air is increased. This means evidently consists in modifying the tension of the vocal cords. When a note is rendered louder and more intense, the vocal cords must be relaxed by remission of the muscular action, in proportion as the force of the current of the breath through the glottis is increased. When a note is rendered fainter, the reverse of this must occur.

The *arches of the palate and the uvula* become contracted during the formation of the higher notes; but their contraction is the same for a note of given height, whether it be falsetto or not; and in either case the arches of the palate may be touched with the finger, without the note being altered. Their action, therefore, in the production of the higher notes seems to be merely the result of involuntary associate nervous action, excited by the voluntarily increased exertion of the muscles of the larynx. If the palatine arches contribute at all to the production of the higher notes of the natural voice and the falsetto, it can only be by their increased tension strengthening the resonance.

The office of the *ventricles of the larynx* is evidently to afford a free space for the vibrations of the lips of the glottis; they may be compared with the cavity at the commencement of the mouth-piece of trumpets, which allows the free vibration of the lips.

Speech.

Besides the musical tones formed in the larynx, a great number of other sounds can be produced in the vocal tubes, between the glottis and the external apertures of the air-passages, the combination of which sounds by the agency of the cerebrum into different groups to designate objects, properties, actions, etc., constitutes *language*. The languages do not employ all the sounds which can be produced in this manner, the combination of some with others being often difficult. Those sounds which are easy of combination enter, for the most part, into the formation of the greater number of languages. Each language contains a certain number of such sounds, but in no one are all brought together. On the contrary, different languages are characterised by the prevalence in them of certain classes of these sounds, while others are less frequent or altogether absent.

Articulate Sounds.—The sounds produced in speech, or *articulate sounds*, are commonly divided into *vowels* and *consonants*: the distinction between which is, that the sounds for the former are generated by the larynx, while those for the latter are produced by interruption of the current of air in some part of the air-passages above the larynx. The term consonant has been given to these because several of them are not properly sounded, except *consonantly with* a vowel. Thus, if it be attempted to pronounce aloud the consonants *b*, *d*, and *g*, or their modifications, *p*, *t*, *k*, the intonation only follows them in their combination with a vowel. To recognize the essential properties of the articulate sounds, we must, according to Müller, first examine them as they are produced in whispering, and then investigate which of them can also be uttered in a modified character conjoined with vocal tone. By this procedure we find two series of sounds: in one the sounds are mute, and cannot be uttered with a vocal tone; the sounds of the other series can be formed independently of voice, but are also capable of being uttered in conjunction with it.

All the vowels can be expressed in a whisper without vocal tone, that is, mutely. These mute vowel-sounds differ, however, in some measure, as to their mode of production, from the consonants. All the mute consonants are formed in the vocal tube above the glottis, or in the cavity of the mouth or nose, by the mere rushing of the air between the surfaces differently modified in disposition. But the sound of the vowels, even when mute, has its source in the glottis, though its vocal cords are not thrown into the vibrations necessary for the production of voice; and the sound seems to be produced by the passage of the current of air between the relaxed vocal cords. The same vowel sound can be produced in the larynx when the mouth is closed, the nostrils being open, and the utterance of all vocal tone avoided. This sound, when the mouth is open, is so modified by varied forms of the oral cavity, as to assume the characters of the vowels *a*, *e*, *i*, *o*, *u*, in all their modifications.

The cavity of the mouth assumes the same form for the articulation of each of the mute vowels as for the corresponding vowel when vocalized; the only difference in the two cases lies in the kind of sound emitted by the larynx. Krantzenstein and Kempelen have pointed out that the conditions necessary for changing one and the same sound into the different vowels, are differences in the size of two parts—the oral canal and the oral opening; and the same is the case with regard to the mute vowels. By oral canal, Kempelen means here the space between the tongue and palate: for the pronunciation of certain vowels both the opening of the mouth and the space just mentioned are widened; for the pronunciation of other vowels both are contracted; and for others one is wide, the other contracted. Admitting five degrees of size, both of the opening of the mouth and of the space between the tongue and palate, Kempelen thus states the dimensions of these parts for the following vowel sounds:—

Vowel.	Sound.	Size of oral opening.	Size of oral canal.
a	as in "far"	5	3
a	,, "name"	4	2
e	,, "theme"	3	1
o	,, "go"	2	4
oo	,, "cool"	1	5

Another important distinction in articulate sounds is, that the utterance of some is only of momentary duration, taking place during a sudden change in the conformation of the mouth, and being incapable of prolongation by a continued expiration. To this class belong *b*, *p*, *d*, and the hard *g*. In the utterance of other consonants the sounds may be *continuous;* they may be prolonged, *ad libitum*, as long as a particular disposition of the mouth and a constant expiration are maintained. Among these consonants are *h*, *m*, *n*, *f*, *s*, *r*, *l*. Corresponding differences in respect to the time that may be occupied in their utterance exist in the vowel sounds, and principally constitute the differences of long and short syllables. Thus the *a* as in "far" and "fate," the *o* as in "go" and "fort," may be indefinitely prolonged; but the same vowels (or more properly different vowels expressed by the same letters), as in "can" and "fact," in "dog" and "rotten," cannot be prolonged.

All sounds of the first or explosive kind are insusceptible of combination with vocal tone ("intonation"), and are absolutely mute; nearly all the consonants of the second or continuous kind may be attended with "intonation."

Ventriloquism.—The peculiarity of speaking, to which the term *ventriloquism* is applied, appears to consist merely in the varied modification of the sounds produced in the larynx, in imitation of the modifications which voice ordinarily suffers from distance, etc. From the observations of Müller and Colombat, it seems that the essential mechanical parts of the process of ventriloquism consist in taking a full inspiration, then keeping the muscles of the chest and neck fixed, and speaking with the mouth almost closed, and the lips and lower jaw as motionless as possible, while air is very slowly expired through a very narrow glottis;

care being taken also, that none of the expired air passes through the nose. But, as observed by Müller, much of the ventriloquist's skill in imitating the voices coming from particular directions, consists in deceiving other senses than hearing. We never distinguish very readily the direction in which sounds reach our ear; and, when our attention is directed to a particular point, our imagination is very apt to refer to that point whatever sounds we may hear.

Action of the Tongue in Speech.—The tongue, which is usually credited with the power of speech—*language* and speech being often employed as synonymous terms—plays only a subordinate, although very important part. This is well shown by cases in which nearly the whole organ has been removed on account of disease. Patients who recover from this operation talk imperfectly, and their voice is considerably modified; but the loss of speech is confined to those letters in the pronunciation of which the tongue is concerned.

Stammering depends on a want of harmony between the action of the muscles (chiefly abdominal) which expel air through the larynx, and that of the muscles which guard the orifice (rima glottidis) by which it escapes, and of those (of tongue, palate, etc.) which modulate the sound to the form of speech.

Over either of the groups of muscles, by itself, a stammerer may have as much power as other people. But he cannot harmoniously arrange their conjoint actions.

CHAPTER XVII.

NUTRITION; THE INCOME AND EXPENDITURE OF THE HUMAN BODY.

The various physiological processes which occur in the human body have, with the exception of those in the nervous and generative systems, which will be considered in succeeding chapters, now been dealt with, and it will be as well to give in this chapter on Nutrition a summary of what has been considered more at length before.

The subject may be considered under the following heads. (1). The Evidence and Amount of Expenditure. (2). The Sources and Amount of Income. (3). The Sources and Objects of Expenditure.

1. **Evidence and Amount of Expenditure.** — The *evidence* of Expenditure by the living body is abundantly complete.

From the table (p. 262) it will be seen how the various amounts of the excreta are calculated.

From the Lungs there is exhaled every 24 hours,

Of Carbonic Acid, about	15,000 grains
„ Water	5,000 „
Traces of organic matter.	
From the Skin—	
Water	11,500 grains
Solid and gaseous matter	250 „
From the Kidneys—	
Water	23,000 grains
Organic matter	680 „
Minerals or salines	420 „
From the Intestines—	
Water	2,000 grains
Various organic and mineral substances	800 „

In the account of Expenditure, must be remembered in addition the milk (during the period of suckling), and the products of secretion from the generative organs (ova, menstrual blood, semen); but, from their variable and uncertain amounts, these cannot be reckoned with the preceding.

Altogether, the Expenditure of the body represented by the sum of these various excretory products amounts every 24 hours to—

Solid and gaseous matter	17,150 grains	(1,113 grms.)
Water (either fluid or combined with the solids and gaseous matter)	49,500 „	(2,695 „)

The matter thus lost by the body is matter the chemical attractions of which have been in great part satisfied; and which remains quite useless as food, until its elements have been again separated and re-arranged by members of the vegetable world (pp. 2 and 3). It is especially instructive to compare the chemical constitution of the products of expenditure, thus separated by the various excretory organs, with that of the sources of income to be immediately considered.

It is evident from these facts that if the human body is to maintain its size and composition, there must be added to it matter corresponding in amount with that which is lost. The income must equal the expenditure.

2. **Sources and Amount of Income.**—The Income of the body consists partly of *Food* and *Drink*, and partly of *Oxygen*.

Into the stomach there is received daily :—

Solid (chemically dry) food	8,000 grains	(520 grms.)
Water (as water, or variously combined with solid food)	35,000-40,000 ,,	(2,444 ,,)

By the Lungs there is absorbed daily :—

Oxygen	13,000 ,,	(844 ,,)

The average total daily receipts, in the shape of food, drink and oxygen, correspond, therefore, with the average total daily expenditure, as shown by the following table.

Income.		*Expenditure.*	
Solid food	8,000 grains	Lungs	20,000 grains.
Water	37,650 ,,	Skin	11,750 ,,
Oxygen	13,000 ,,	Kidneys	24,100 ,,
		Intestines	2,800 ,,
	58,650 grains	(Generative and mammary-gland products are supposed to be included.)	
(about 3.808 grms., or 8⅓lb.)			58,650 grains
			(About 3808 grms.)

These quantities are approximate only. But they may be taken as fair averages for a healthy adult. The absolute identity of the two numbers (in *grains*) in the two tables is of course diagrammatic. No such exactitude in the account occurs in any living body, in the course of any given twenty-four hours. But any difference which exists between the two amounts of *income* and *expenditure* at any given period, corresponds merely with the slight variations, in the amount of *capital*, (weight of body) to which the healthiest subject is liable.

The chemical composition of the food (p. 264) may be profitably compared with that of the excreta, as before mentioned. The greater part of our food is composed of matter, which contains much potential energy; and in the chemical changes (combustion and other processes), to which it is subject in the body, active energy is manifested.

3. **The Sources and Objects of Expenditure.**—The sources of necessary waste and expenditure in the living body are various and extensive. They may be comprehended under the following heads:—(1) *Common wear and tear;* such as that to which all structures, living and not living, are subjected by exposure and work; but which must be especially large in the soft and easily decaying structures of an animal body.

(2) *Manifestations of Force in the form either of Heat or Motion.* In the former case (Heat), the combustion must be sufficient to maintain a temperature of about 100° F. (37·8° C.) throughout the whole substance of the body, in all varieties of external temperature, notwithstanding the large amount continually lost in the ways previously enumerated (p. 387). In the case of Motion, there is the expenditure involved in (*a*) Ordinary muscular movements, as in Prehension, Mastication, Locomotion, and numberless other ways: (*b*) Various involuntary movements, as in Respiration, Circulation, Digestion, &c.

(3) *Manifestation of Nerve-force;* as in the general regulation of all physiological processes, *e.g.*, Respiration, Circulation, Digestion; and in Volition and all other manifestations of cerebral activity.

(4) *The energy expended in all physiological processes, e.g.*, Nutrition, Secretion, Growth, and the like.

The Total expenditure or manifestation of energy by an animal body can be measured, with fair accuracy; the terms used being such as are employed in connection with other than vital operations. All statements, however, must be considered for the present approximate only, and especially is this the case with respect to the comparative share of expenditure to be assigned to the various objects just enumerated.

The amount of energy daily manifested by the adult human body in (*a*) the maintenance of its temperature; (*b*) in internal mechanical work, as in the movements of the respiratory muscles, the heart, &c.; and (*c*) in external mechanical work, as in locomotion and all other voluntary movements, has been reckoned at about 3,400 foot-tons (p. 154). Of this amount only one-tenth is directly expended in internal and external mechanical work; the remainder being employed in the maintenance of the body's heat. The latter amount represents the heat which would be required to raise 48·4 lb. of water from the freezing to the boiling point; or if converted into mechanical power, it would suffice to raise the body of a man weighing about 150 lb. through a vertical height of 8½ miles.

To the foregoing amounts of expenditure must be added the quite unknown quantity expended in the various manifestations of nerve-force, and in the work of nutrition and growth (using these terms in their widest sense). By comparing the amount of energy which should be produced in the body from so much food of a given kind, with that which is actually manifested (as shown by the various products of combustion, in the excretions) attempts have been made, indeed, to estimate, by a process of exclusion, these unknown quantities; but all such calculations must be at present considered only very doubtfully approximate.

Sources of Error.—Among the sources of error in any such calculations must be reckoned, as a chief one, the, at present, entirely unknown extent to which forces external to the body (mainly heat) can be utilised by the tissues. We are too apt to think that the heat and light of the sun are directly correlated, as far as living beings are concerned, with the chemico-vital transformations involved in the nutrition and growth of the members of the vegetable world only. But animals, although comparatively independent of external heat and other forces, probably utilise them, to the degree occasion offers. And although the *correlative* manifestation of energy in the body, due to external heat and light, may still be measured in so far as it may take the form of mechanical work; yet, in so far as it takes the form of expenditure in nutrition or nerve-force, it is evidently impossible to include it by any method of estimation yet discovered; and all accounts of it must be matters of the purest theory. These considerations may help to explain the apparent discrepancy between the amount of energy which is capable of being produced by the usual daily amount of food, with that which is actually manifested daily by the body; the former leaving but a small margin for anything beyond the maintenance of heat, and mechanical work.

In the foregoing sketch we have supposed that the excreta are exactly replaced by the ingesta.

Nitrogenous Equilibrium and Formation of Fat.

If an animal, which has undergone a starving period, be fed upon a diet of lean meat, it is found that instead of the greater part of the nitrogen being stored up, as one would expect, the chief part of it appears in the urine as urea, and on continuing with the diet the excreted nitrogen approximates more and more closely to the ingested nitrogen until at last the amounts are equal in both cases. This is called *nitrogenous equilibrium*. There may, however, be at the same time an increase of weight which is due to the putting on of fat. If this is the case it must be apparent that the protoplasm of the tissues is able to form fat out of proteid material and to split it up into urea and fat. If fat be given in small quantities with the meat, for a time the carbon of the egesta and ingesta are equal, but if the fat be increased beyond a certain point the body weight increases from a deposition of fat; not, however, by a mere mechanical deposition or filtration from the blood, but by an actual act of secretion by the protoplasm whereby the fat globules are stored up within itself. In a similar manner as regards carbo-hydrates, if they are in small quantity, the whole of the carbon appears in the excreta, but beyond a certain amount a considerable portion of it is retained in fat, having been by the protoplasm stored up within itself in that material. The amount of proteid material required to produce nitrogenous equilibrium is considerable, but it may be materially diminished by the addition of carbo-hydrate or fatty food or of gelatine to the exclusively meat diet.

It is of much interest to consider how the protoplasm acts in converting food into energy and decomposition products, since the substance itself does not undergo much change in the process except a slight amount of wear and tear. We may assume that it is the property of protoplasm to separate from the blood the materials which may be required to produce secretions, in the case of the protoplasm of secreting glands, or to evolve heat and energy, as in the case of the protoplasm of muscle. The substances are very possibly different for each process, and the decomposition products, too, may be different in quality or quantity. Proteid materials appear to be specially needed, as is shown by the invariable presence of urea in the urine even during starvation; and as in the latter case, there has been no food from which these materials could have been derived, the urea is considered to be derived from the disintegration of the nitrogenous tissues themselves. The removal of all fat from the body in a starvation period, as the first apparent change, would lead to the supposition that fat is also a specially necessary pabulum for the production of protoplasmic energy; and the fact that, as mentioned above, with a diet of lean meat an enormous amount appears to be required, suggests that in that case protoplasm obtains the fat it needs from the proteid food, which process must be evidently a source of much waste of nitrogen. The idea that proteid food has two destinations in the economy, viz., to form organ or tissue proteid which builds up organs and tissues, and circulating proteid, from which the organs and tissues derive the materials of their secretions or for producing their energy, is a convenient one, as it is unlikely that protoplasm would go to the expense of construction simply for the sake of immediate destruction.

CHAPTER XVIII.

THE NERVOUS SYSTEM.

Chief Divisions of the Nervous System.—The Nervous System consists of two portions or systems, the (1) *Cerebro-spinal*, and the (2) *Sympathetic*.

(I.) The *Cerebro-spinal* system includes the Brain and Spinal cord, with the nerves proceeding from them. Its fibres are chiefly, but not exclusively, distributed to the skin and other organs of the senses, and to the voluntary muscles.

(II.) The *Sympathetic* Nervous system consists of:—(1) A double chain of ganglia and fibres, which extends from the cranium to the pelvis, along each side of the vertebral column, and from which branches are distributed both to the cerebro-spinal system, and to other parts of the sympathetic system. With these may be included the small ganglia in connection with those branches of the fifth cerebral nerve which are distributed in the neighbourhood of the organs of special sense: namely, the *ophthalmic*, *otic*, *spheno-palatine*, and *submaxillary*-ganglia. (2) Various ganglia and plexuses of nerve-fibres which give off branches to the thoracic and abdominal viscera, the chief of such plexuses being the *Cardiac*, *Solar*, and *Hypogastric ;* but in intimate connection with these are many secondary plexuses, as the *aortic*, *spermatic*, and *renal*. To these plexuses, fibres pass from the prævertebral chain of ganglia, as well as from cerebro-spinal nerves. (3) Various ganglia and plexuses in the substance of many of the viscera, as in the *stomach*, *intestines*, and *urinary bladder*. These, which are, for the most part, microscopic, also freely communicate with other parts of the sympathetic system, as well as, to some extent, with the cerebro-spinal. (4) By many, the ganglia on the *posterior roots of the spinal nerves*, on the *glosso-pharyngeal* and *vagus*, and on the *sensory root* of the *fifth cerebral nerve* (Gasserian ganglion), are also included as sympathetic-nerve structures.

Elementary Structure.—The organs both of the Cerebro-spinal and Sympathetic nervous systems are composed of two structural elements—*fibres* and *cells.* The cells are collected in masses, and are always mingled, more or less, with fibres; such a collection of cellular and fibrous nerve-structure being termed a *nerve-centre.* The fibres, besides entering into the composition of nerve-centres, form by themselves the *nerves*, which connect the various centres, and are distributed in the several parts of the body.

Nerve Fibres.

Structure.—Each nerve-trunk is composed of a variable number of different-sized bundles (*funiculi*) of nerve-fibres which have a special sheath (*perineurium* or *neurilemma*). The funiculi are enclosed in a firm fibrous sheath (*epineurium*); this sheath also sends in processes of connective tissue which connect the bundles together. In the funiculi between the fibres is a delicate supporting tissue (the *endoneurium*).

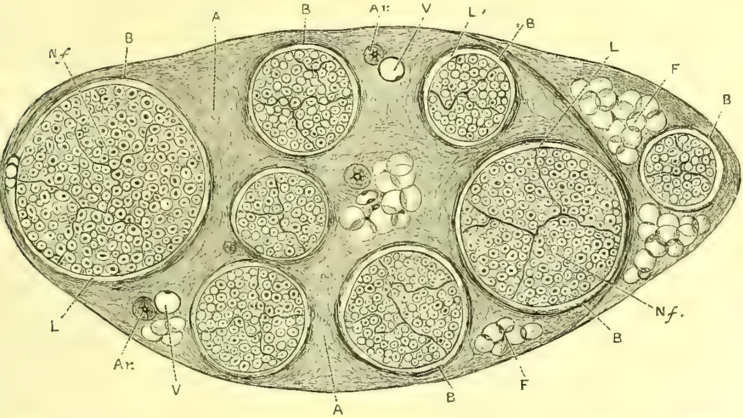


Fig. 302.—*Transverse section of the sciatic nerve of a cat* × 100.—It consists of bundles (*Funiculi*) of nerve-fibres ensheathed in a fibrous supporting capsule. *epineurium*, A; each bundle has a special sheath (not sufficiently worked out from the *epineurium* in the figure) or *perineurium* B; the nerve-fibres N *f* are separated from one another by *endoneurium*; L, lymph spaces; Ar, artery; V, vein; F, fat. (V. D. Harris.)

There are numerous lymph-spaces both beneath the connective-tissue investing individual nerve-fibres, and also beneath that which surrounds the funiculi.

Varieties.—In most nerves, two kinds of fibres are mingled; those of one kind being most numerous in, and characteristic of, nerves of the Cerebro-spinal system; those of the other, most numerous in nerves of the Sympathetic system. These are called (A) medullated or white fibres, and (B) non-medullated or grey fibres.

(A). **Medullated Fibres.**—Each medullated nerve-fibre is made up of the following parts:—(1.) Primitive nerve sheath, or nucleated sheath of Schwann. (2) Medullary sheath, or white substance of Schwann. (3) Axis-cylinder, primitive band, axis band, or axial fibre.

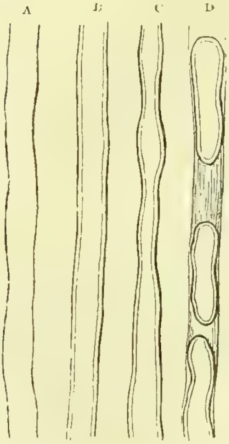


Fig. 303. — *Primitive nerve-fibres.* A. A perfectly fresh tubule with a single dark outline. B. A tubule or fibre with a double contour from commencing post-mortem change. C. The changes further advanced, producing a varicose or beaded appearance. D. A tubule or fibre, the central part of which, in consequence of still further changes, has accumulated in separate portions within the sheath (Wagner).

Although these parts can be made out in nerves examined some time after death, in a recent specimen the contents of the sheath appear to be homogeneous. But by degrees they undergo changes which show them to be composed of two different materials. The internal or central part, occupying the axis of the tube (*axis-cylinder*), becomes greyish, while the outer, or cortical portion (*white substance of Schwann*), becomes opaque and dimly granular or grumous, as if from a kind of coagulation. At the same time, the fine outline of the previously transparent cylindrical tube is exchanged for a dark double contour (fig. 303, B), the outer line being formed by the sheath of the fibre, the inner by the margin of curdled or coagulated medullary substance. The granular material shortly collects into little masses, which distend portions of the tubular membrane; while the intermediate spaces collapse, giving the fibres a varicose, or beaded appearance (fig. 303, C and D), instead of the previous cylindrical form. The whole contents of the nerve-tubules are extremely soft, for when subjected to pressure they readily pass from one part of the tubular sheath to another, and often cause a bulging at the side of the membrane. They also readily escape, on pressure, from the extremities of the tubule, in the form of a grumous or granular material.

The *nucleated sheath of Schwann* is a pellucid membrane, forming the outer investment of the nerve-fibre. Within this delicate structureless membrane nuclei are seen at intervals, surrounded by a variable amount of protoplasm. The sheath is structureless, like the sarcolemma, and the nuclei appear to be within it: together with the protoplasm which surrounds them, they are the relics of embryonic cells, and from their resemblance to the muscle corpuscles of striated muscle, may be termed nerve-corpuscles.

(2.) The *medullary sheath* or *white substance of Schwann* is the part to which the peculiar white aspect of the cerebro-spinal nerves is principally due. It is a thick, fatty, semi-fluid substance, as we have seen, possessing a double contour. It is said to be made up of a fine reticulum (Stilling, Klein), in the meshes of which is embedded the bright fatty material.

According to M'Carthy, the medullary sheath is composed of small rods radiating from the axis-cylinder to the sheath of Schwann. Sometimes the whole space is occupied by these rods, whilst at other times the rods appear shortened, and compressed laterally into bundles embedded in some homogeneous substance.

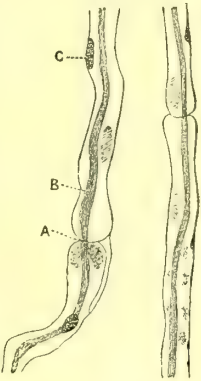


Fig. 304.—*Two nerve-fibres of sciatic nerve.* A. Node of Ranvier. B. Axis-cylinders. C. Sheath of Schwann, with nuclei. × 300. (Klein and Noble Smith.)

(3.) The *axis-cylinder* consists of a large number of primitive *fibrillæ*. This is well shown in the cornea, where the axis-cylinders of nerves break up into minute fibrils which go to form terminal networks (see Cornea), and also in the spinal cord, where these fibrillæ form a large part of the grey matter. From various considerations, such as its invariable presence and unbroken continuity in all nerves, though the primitive sheath or the medullary sheath may be absent, there can be little doubt that the axis-cylinder is the conductor of nerve-force, the other parts of the nerve having the subsidiary function of support and possibly of insulation.

At regular intervals in most medullated nerves, the nucleated sheath of Schwann possesses annular constrictions (nodes of

Ranvier). At these points (figs. 304, 305), the continuity of the medullary white substance is interrupted, and the primitive sheath comes into immediate contact with the axis-cylinder.

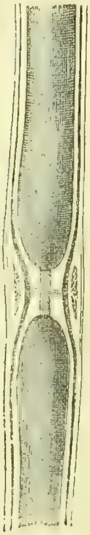


Fig. 305.—*A node of Ranvier in a medullated nerve-fibre*, viewed from above. The medullary sheath is interrupted, and the primitive sheath thickened. Copied from Axel Key and Retzius. × 750. (Klein and Noble Smith.)

Size. — The size of the nerve-fibres varies, and the same fibres do not preserve the same diameter through their whole length, being largest in their course within the trunks and branches of the nerves, in which the majority measure from $\frac{1}{2000}$ to $\frac{1}{3000}$ of an inch in diameter. As they approach the brain or spinal cord, and generally also in the tissues in which they are distributed, they gradually become smaller. In the grey or vesicular substance of the brain or spinal cord, they generally do not measure more than from $\frac{1}{10000}$ to $\frac{1}{14000}$ of an inch.

(B.) **Non-medullated Fibres.** — The fibres of the second kind (fig. 306), which constitute the whole of the branches of the *olfactory* and *auditory* nerves, the principal part of the trunk and branches of the *sympathetic nerves*, and are mingled in various proportions in the cerebro-spinal nerves, differ from the preceding, chiefly in their fineness, being only about $\frac{1}{2}$ or $\frac{1}{3}$ as large in their course within the trunks and branches of the nerves; in the absence of the double contour; in their contents being apparently uniform; and in their having, when in bundles, a yellowish grey hue instead of the whiteness of the cerebro-spinal nerves. These peculiarities depend on their not possessing the outer layer of medullary nerve-substance; their contents being composed exclusively of the axis-cylinder. Yet, since many nerve-fibres may be found which appear intermediate in character between these two kinds, and since the large fibres, as they approach both their central and their peripheral end, gradually diminish in size, and assume many of the other characters of the fine fibres of the sympathetic system, it is not necessary to suppose that there is any material difference in the two kinds of fibres.

It is worthy of note, that in the fœtus, at an early period of development, all nerve-fibres are non-medullated.

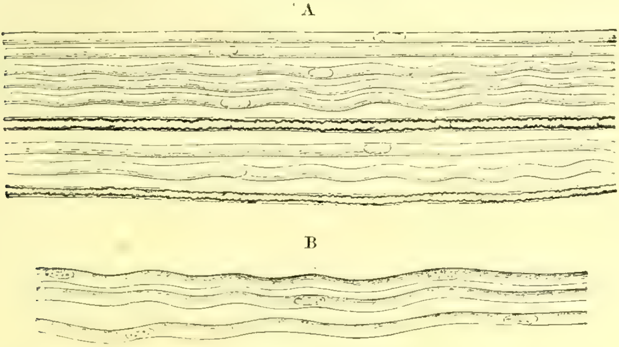


Fig. 306.—*Grey, pale, or gelatinous nerve-fibres.* A. From a branch of the olfactory nerve of the sheep; *a*, *a*, two dark-bordered or white fibres from the fifth pair, associated with the pale olfactory fibres. B. From the sympathetic nerve. × 450 (Max Schultze).

Course.—Every nerve-fibre in its course proceeds uninterruptedly from its origin in a nerve-centre to near its destination, whether this be the periphery of the body, another nervous centre, or the same centre whence it issued.

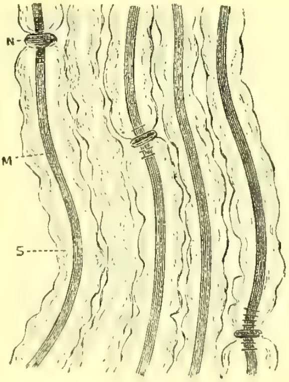


Fig. 307.—*Several fibres of a bundle of medullated nerve-fibres* acted upon by silver nitrate to show peculiar behaviour of nodes of Ranvier towards their reagent. The silver has penetrated at the nodes, and has stained the axis-cylinder for a short distance. (Klein and Noble Smith.)

Bundles of fibres run together in the nerve-trunk, but merely lie in apposition with each other; they do not unite: even when they anastomose, there is no union of fibres, but only an interchange of fibres between the anastomosing funiculi. Although each nerve-fibre is thus single and undivided through nearly its whole course, yet as it approaches the region in which it terminates, individual fibres break up into several subdivisions (fig. 308) before their final ending. The medullated nerve-fibres, moreover, lose their medullary sheath before their final distribution, and acquire the characters more or less of non-medullated fibres.

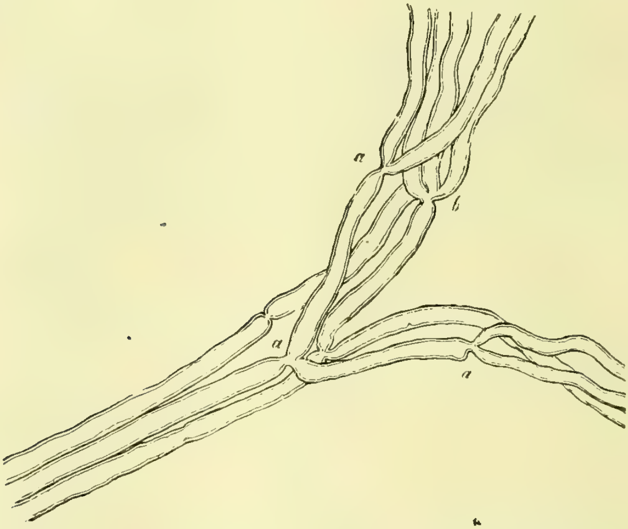


Fig. 308.—*Small branch of a muscular nerve of the frog,* near its termination, showing divisions of the fibres. *a*, into two; *b*, into three; × 350 (Kölliker).

Plexuses.—At certain parts of their course, nerves form *plexuses*, in which they anastomose with each other, as in the case of the brachial and lumbar plexuses. The objects of such interchange of fibres are, (*a*), to give to each nerve passing off from the plexus, a wider connection with the spinal cord than it would have if it proceeded to its destination without such communication with other nerves. Thus, each nerve by the wideness of its connections, is less dependent on the integrity of any single portion, whether of nerve-centre or of nerve-trunk, from which it may spring. (*b*) Each part supplied from a plexus has wider relations with the nerve-centres, and more extensive sympathies; and, by means of the same arrangement, groups of muscles may be co-ordinated, every member of the group receiving motor filaments from the same parts of the nerve-centre. (*c*) Any given part, say a limb, is less dependent upon the integrity of any one nerve. (*d*) A plexus is frequently the means by which *centripetal* and *centrifugal* fibres are conveniently mingled for distribution, as in the case of the pneumogastric nerve, which receives motor filaments, near its origin, from the spinal accessory.

As medullated nerve-fibres approach their terminations they lose their medullary sheath, and consist then merely of axis-cylinder and primitive sheath. They then lose also the latter, and only the axis-cylinder is left with here and there a nerve-corpuscle partly rolled around it. Finally, even this investment ceases, and the axis-cylinder breaks up into its elementary fibrillæ.

Peripheral Nerve Terminations.

(a.) **Sensory.**—(1.) *Pacinian Corpuscles.*—The Pacinian bodies or corpuscles (figs. 309 and 310), named after their discoverer Pacini, are little elongated oval bodies, situated on some of the cerebro-spinal and sympathetic nerves, especially the cutaneous nerves of the hands and feet; and on branches of the large sympathetic plexus about the abdominal aorta (Kölliker). They often occur also on the nerves of the mesentery, and are especially well seen in the mesentery of the cat. They have been observed also in the pancreas, lymphatic glands and thyroid glands, as well as in the penis of the cat. Each corpuscle is attached by a narrow pedicle to the nerve on which it is situated, and is formed of several concentric layers of fine membrane, consisting of a hyaline ground-membrane with connective tissue fibres, each layer being lined by endothelium (fig. 310); through its pedicle passes a single nerve-fibre, which, after traversing the several concentric layers and their immediate spaces, enters a central cavity, and, gradually losing its dark border, and becoming smaller, terminates at or near the distal end of the cavity, in a knob-like enlargement, or in a bifurcation. The enlargement commonly found at the end of the fibre, is said by Pacini to resemble a ganglion corpuscle; but this

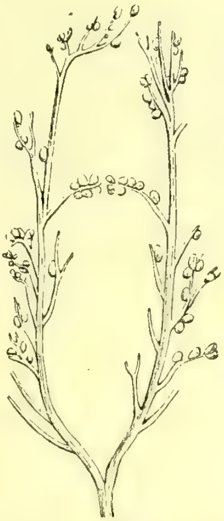


Fig. 309.—*Extremities of a nerve of the finger with Pacinian corpuscles* attached, about the natural size (adapted from Henle and Kölliker).

observation has not been confirmed. In some cases two nerves have been seen entering one Pacinian body, and in others a nerve after passing unaltered through one, has been observed to terminate in a second Pacinian corpuscle. The physiological import of these bodies is still obscure. Closely allied to Pacinian corpuscles, except that they are smaller and longer, with a row of nuclei around the central termination of the nerve in the core, are *corpuscles of Herbst*, which have been found chiefly in the tongues of ducks. The capsules are nearer together, and towards the centre the endothelial sheath appears to be absent.

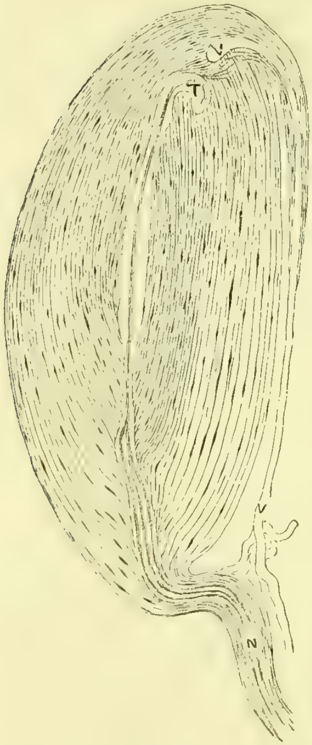


Fig. 310.—*Pacinian corpuscle of the cat's mesentery.* The stalk consists of a nerve-fibre (N) with its thick outer sheath. The peripheral capsules of the Pacinian corpuscle are continuous with the outer sheath of the stalk. The intermediary part becomes much narrower near the entrance of the axis-cylinder into the clear central mass. A hook-shaped termination with the end-bulb (T) is seen in the upper part. A blood-vessel (V) enters the Pacinian corpuscle, and approaches the end-bulb; it possesses a sheath which is the continuation of the peripheral capsules of the Pacinian corpuscle. × 100. (Klein and Noble Smith.)

(2.) *End-bulbs* are found in the conjunctiva, in the penis and clitoris, in the skin, and in tendon; each is composed of a medullated nerve-fibre which terminates in corpuscles of various shapes, with a capsule containing a transparent or striated mass, in the centre of which terminates the axis-cylinder of the nerve-fibre, the ending of which is somewhat clubbed (fig. 230).

(3.) *Touch corpuscles* (fig. 229) are found in the papillæ of the skin or among its epithelium; they may be simple or compound; when simple they are large and slightly flattened transparent nucleated ganglion cells enclosed in a capsule; when compound the capsule contains several small cells.

The corpuscles of Grandry form another variety, and have been noticed in the beaks and tongues of birds. They consist of corpuscles oval or spherical, contained within a delicate nucleated sheath, and containing several cells, two or more compressed vertically. The cells are granular and transparent, with a nucleus. The nerve enters on one side, and laying aside its medullary sheath, terminates in or between the cells.

(4.) In *plexuses*, as in the cornea, both sub-epithelial and also intra-epithelial.

(5.) In cells, as in the salivary glands (p. 282), and in the special sense organs. To the latter, further allusion will be made in a future chapter.

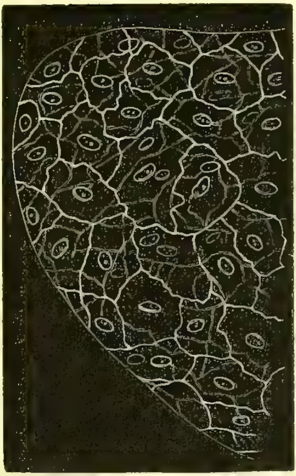


Fig. 311.—*Summit of a Pacinian corpuscle of the human finger,* showing the endothelial membranes lining the capsules. × 220. (Klein and Noble Smith.)

(b.) **Motory**—(1.) In *unstriped* muscle, the nerves first of all form a plexus, called the *ground plexus* (Arnold), corresponding to each group of muscle bundles; the plexus is made by the anastomosis of the primitive fibrils of the axis-cylinders. From the ground plexus, branches pass off, and again anastomosing, form plexuses which correspond to each muscle bundle,—*intermediary plexuses.* From these plexuses branches consisting of primitive fibrils pass in between the individual fibres and anastomose. These fibrils either send off finer branches, or terminate themselves in the nuclei of the muscle cells.

(2.) In *striped* muscle the nerves end in the so-called "*motorial end-plates,*" having first formed, as in the case of unstriped fibres, ground and intermediary plexuses. The nerves are, however, medullated, and when a branch of the intermediary plexus passes to enter a muscle-fibre, its primitive sheath becomes continuous with the sarcolemma, and the axis-cylinder forms a network of its fibrils on the surface of the fibre. This network lies embedded in a flattened granular mass containing nuclei of several kinds; this is the *motorial end-plate* (fig. 312). In batrachia, besides end-plates, there is another way in which the nerves end in the muscle-fibres, viz., by rounded extremities, to which oblong nuclei are attached.

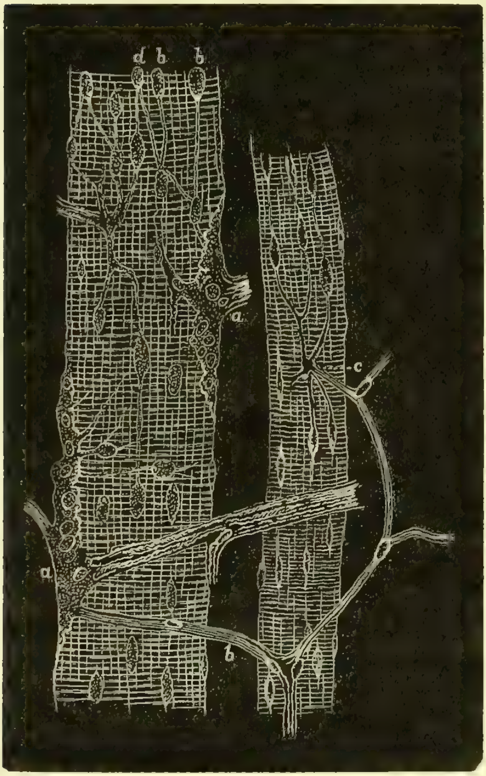


Fig. 312.—*Two striped muscle-fibres of the hyoglossus of frog.* *a*, Nerve end-plate; *b*, nerve fibres leaving the end-plate; *c*, nerve-fibres, terminating after dividing into branches; *d*, a nucleus in which two nerve-fibres anastomose. × 600. (Arndt.)

Nerve Cells or Corpuscles.

The *vesicular* nervous substance contains, as its name implies, *vesicles* or *corpuscles*, in addition to fibres; and a structure, thus composed of corpuscles and inter-communicating fibres, constitutes a *nerve-centre;* the chief nerve-centres being the grey matter of the brain and spinal cord, and the various *ganglia*. In the brain and spinal cord a fine stroma of *neuroglia* (p. 41), extends throughout both the fibrous and vesicular nervous substance, and forms a supporting and investing framework for the whole.

The nerve-corpuscles which give to the ganglia and to certain parts of the brain and spinal cord the peculiar greyish or reddish-grey aspect by which these parts are characterised, are large, nucleated cells, filled with a finely granular material, some of which is often dark like pigment: the nucleus containing a nucleolus. Besides varying much in shape, partly in consequence of mutual pressure, they present such other varieties as make it probable either that there are two different kinds, or that, in the stages of their development, they pass through very different forms. Some of them are small, general spherical or ovoid, and have a regular uninterrupted outline. These *simple* nerve-corpuscles are most numerous in the sympathetic ganglia; each is enclosed in a nucleated sheath. Others, which are called *caudate* or *stellate nerve-corpuscles* (fig. 313), are larger, and have one, two, or more long processes issuing from them, the cells being called respectively *unipolar*, *bipolar*, or *multipolar;* which processes often divide and subdivide, and appear tubular, and filled with the same kind of granular material that is contained within the corpuscle. Of these processes some appear to taper to a point and terminate at a greater or less distance from the corpuscle; some appear to anastomose with similar offsets from other corpuscles; while others are continuous with nerve-fibres, the prolongation from the cell by degrees assuming the characters of the nerve-fibre with which it is continuous.

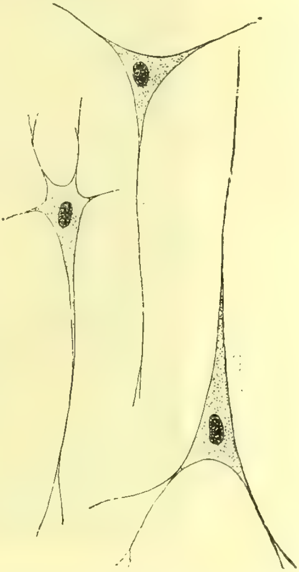


Fig. 313.—*Ganglion nerve-corpuscles* of different shapes. (Klein and Noble Smith.)

Ganglion-cells are each enclosed in a transparent membranous capsule similar in appearance to the nucleated sheath of Schwann in nerve-fibres: within this capsule is a layer of small flattened cells.

That process of a nerve-cell which becomes continuous with a nerve-fibre is always unbranched, as it leaves the cell. It at first has all the characters of an axis-cylinder, but soon acquires a medullary sheath, and then may be termed a nerve-fibre. This continuity of nerve-cells and fibres may be readily traced out in the anterior cornua of the grey matter of the spinal cord. In many large branched nerve-cells a distinctly fibrillated appearance is observable; the fibrillæ are probably continuous with those of the axis-cylinder of a nerve.

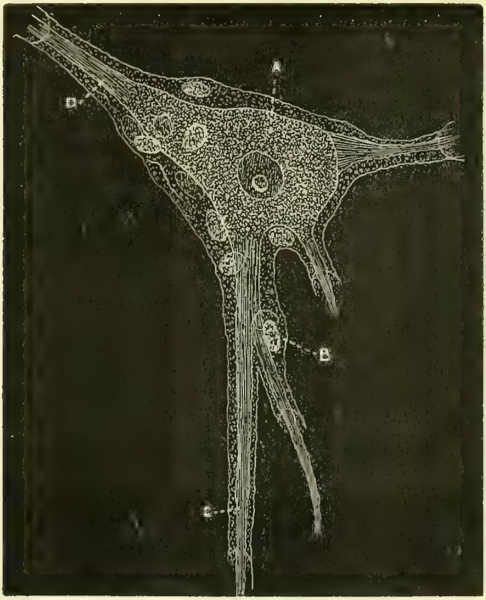


Fig. 314.—*An isolated sympathetic ganglion cell of man*, showing sheath with nucleated-cell lining, B. A. Ganglion-cell, with nucleus and nucleolus. C. Branched process. D. Unbranched process. Copied from Key and Retzius. × 750. (Klein and Noble Smith).

The Functions of Nerve Fibres.

It will be evident from the account of nervous action previously given (p. 513 *et seq.*) that nerve-fibres are stimulated to act by anything which increases their irritability, but that they are incapable of originating of themselves the condition necessary for the manifestation of their own functions. When a cerebro-spinal nerve-fibre is irritated in the living body as by pinching, or by heat, or by electrifying it, there is, under ordinary circumstances, one of two effects,—either there is pain, or there is twitching of one or more muscles to which the nerve distributes its fibres. From various considerations it is certain that pain is always the result of a change in the nerve-cells of the brain. Therefore, in such an experiment as that referred to, the irritation of the nerve-fibre seems to the experimenter to be *conducted* in one of two directions, *i.e.*, either to the brain (*central termination of the fibre*), when there is pain, or to a muscle (*peripheral termination*) when there is movement.

The effect of this simple experiment is a type of what always occurs when nerve-fibres are engaged in the performance of their functions. The result of stimulating them, which roughly imitates what happens naturally in the body, is found to occur at one or other of their extremities, central or peripheral, never at both; and in accordance with this fact, and because, for any given nerve-fibre, the result is always the same, nerves are commonly classed as *sensory* or *motor*.

It may be well to state, in order to avoid confusion, that the apparent conduction in *both* directions, which seems to occur when a nerve, say the ulnar or median is irritated, depends on the fact that both motor and sensory *fibres* are bound up together in the same *nerve-trunks*—an arrangement which, for medium-sized and large nerves, is the rule rather than the exception.

Conduction in Nerves.—A nerve when removed from the body will be found to conduct electrical impressions in either direction equally well, and microscopic examination fails to discover the slightest essential difference between motor and sensory nerve-fibres. The question therefore, naturally arises whether the conduction of a stimulus in the living body, in one direction only, is not rather apparent than real, the difference in the result being due to the different connections of the two kinds of nerve-fibres respectively at their extremities. In other words, when the stimulation of a nerve-fibre causes pain, the result is due to its *central* extremity being in connection with structures which alone can give rise to the sensation, while its *peripheral* extremity, although the stimulus is equally conducted to it, has no connection with a structure which can respond to the irritation in any manner sensible to the observer. So, when motion is the result of a like irritation, it is because the *peripheral* extremity of the nerve-fibre is in connection with muscles which will respond by contracting, while its *central* extremity, although equally stimulated, has no means of showing the fact by any evident result.

That this is the true explanation is made highly probable, not merely by the absence of any structural differences in the two kinds of nerve-fibre, but also by the fact, proved by direct experiment, that if a centripetal nerve (gustatory) be divided, and its central portion be made to unite with the distal portion of a divided motor nerve (hypoglossal) the effect of irritating the former after the parts have healed, is to excite contraction in the muscles supplied by the latter. (Philippeaux and Vulpian.)

Classification of Nerve-Fibres.—1. Centripetal, afferent, or 2. Centrifugal, efferent, or motor. 3. Intercentral.

Centripetal or *afferent*, and *centrifugal* or *efferent* are frequently employed in connection with nerve-fibres in lieu of the corresponding terms *sensory* and *motor*, because the result of stimulating a nerve of the former kind is not *always* the production of pain or other form of sensation, nor is motion the *invariable* result of stimulating the latter.

Conduction in *centripetal* nerves may cause (*a*) pain, or some other kind of sensation; or (*b*) reflex action; or (*c*) inhibition, or restraint of action.

Conduction in *centrifugal* nerves may cause (*a*) contraction of muscle (p. 490), (motor nerves); or (*b*) it may influence nutrition (trophic nerves); or (*c*) may influence secretion (secretory nerves).

The term *intercentral* is applied to those nerve-fibres which connect more or less distinct nerve-centres, and may, therefore be said to have no *peripheral* distribution, in the ordinary sense of the term.

It is a law of action in all nerve-fibres, and corresponds with the continuity and simplicity of their course, that an impression made on any fibre, is simply and uninterruptedly transmitted along it, without being imparted or diffused to any of the fibres lying near it. In other words, all nerve-fibres are mere *conductors* of impressions. Their adaptation to this purpose is, perhaps, due to the contents of each fibre being completely isolated from those of adjacent fibres by the membrane or sheath in which each is enclosed, and which acts, it may be supposed, just as silk, or other non-conductors of electricity do, which, when covering a wire, prevent the electric condition of the wire from being conducted into the surrounding medium.

Velocity of Nerve-force. — The change which a stimulus sets upon a nerve, of the exact nature of which we are unacquainted, appears to travel along a nerve-fibre in both directions in the form of a wave. Nervous force travels along nerve-fibres with considerable velocity. Helmholtz and Baxt have estimated the average rate of conduction in human motor nerves at 111 feet (nearly 29 metres) per second; this result agreeing very closely with that previously obtained by Hirsch. Rutherford's observations agree with those of Von Wittich, that the rate of transmission in sensory nerves is about 140 feet per second.

Conduction in Sensory Nerves.—Centripetal nerves *appear* (p. 553) able to convey impressions only from the parts in which they are distributed, towards the nerve-centre from which they arise, or to which they tend. Thus, when a sensitive nerve is divided, and irritation is applied to the end of the proximal portion, *i.e.*, of the portion still connected with the nervous centre, sensation is perceived, or a reflex action ensues; but, when the end of the distal portion of the divided nerve is irritated, no effect appears. When an impression is made upon any part of the course of a sensory nerve, the mind may perceive it as if it were made not only upon the point to which the stimulus is applied, but also upon all the points in which the fibres of the irritated nerve are distributed: in other words, the effect is the same as if the irritation were applied to the parts supplied by the branches of the nerve. When the whole trunk of the nerve is irritated, the sensation is felt at all the parts which receive branches from it; but when only individual portions of the trunk are irritated, the sensation is perceived at those parts only which are supplied by the several portions. Thus, if we compress the ulnar nerve where it lies at the inner side of the elbow-joint, behind the internal condyle, we have the sensation of "pins and needles," or of a shock, in the parts to which its fibres are distributed, namely, in the palm and back of the hand, and in the fifth and ulna half of the fourth finger. When stronger pressure is made, the sensations are felt in the fore-arm also; and if the mode and direction of the pressure be varied, the sensation is felt by turns in the fourth finger, in the fifth, and in the palm of the hand, or in the back of the hand, according as different fibres or fasciculi of fibres are more pressed upon than others.

Illustrations.—It is in accordance with this law, that when parts are deprived of sensibility by compression or division of the nerves supplying them, irritation of the portion of the nerve connected with the brain still excites sensations which are felt as if derived from the parts to which the peripheral extremities of the nerve-fibres are distributed. Thus, there are cases of paralysis in which the limbs are totally insensible to external stimuli, yet are the seat of most violent pain, resulting apparently from irritation of the sound part of the trunk of the nerve still in connection with the brain, or from irritation of those parts of the nervous centre from which the sensory nerve or nerves which supply the paralysed limbs originate. An illustration of the same law is also afforded by the cases in which division of a nerve for the cure of neuralgic pain is found useless, and in which the pain continues or returns, though portions of the nerves be removed. In such cases, the disease is probably seated nearer the nervous centre than the part at which the division of the nerve is made, or it may be in the nervous centre itself. In the same way may be explained the fact, that when part of a limb has been removed by amputation, the remaining portions of the nerves may give rise to sensations which the mind refers to the lost part. When the stump is healed, the sensations which we are accustomed to have in a sound limb are still felt; and tingling and pains are referred to the parts that are lost, or to particular portions of them, as to single toes, to the sole of the foot, to the dorsum of the foot, etc.

It must not be assumed, as it often has been, that the mind has no power of discriminating the very point in the length of any nerve-fibre to which an irritation is applied. Even in the instances referred to, the mind perceives the pressure of a nerve at the point of pressure, as well as in the seeming sensations derived from the extremities of the fibres: and in stumps, pain is felt in the stump, as well as, seemingly, in the parts removed. It is not quite certain whether those sensations are due to conduction through the nerve fibres which are on their way to be distributed elsewhere, or through the sentient extremities of nerves which are themselves distributed to the many trunks of the nerves, the *nervi nervorum.* The latter is the more probable supposition.

When, in a part of the body which receives two sensory nerves, one is paralysed, the other may or may not be inadequate to maintain the sensibility of the entire part; the extent to which the sensibility is preserved corresponding probably with the number of the fibres unaffected by the paralysis. There are instances in which the trunk of the chief sensory nerve supplied to a part having been divided, the sensibility of the part is still preserved by intercommunicating fibres from a neighbouring nerve-trunk.

Conduction in the Nerves of Special Sense.—The laws of conduction in the *olfactory*, *optic*, *auditory*, *gustatory*—resemble in many aspects those of conduction in the nerves of common sensation, just described. Thus the effect is always *central;* stimulation of the trunk of the nerve produces the same effect as that of its extremities, and if the nerve be severed, it is the central and not the peripheral extremity which responds to irritation, although the sensation is referred to the periphery. There are, however, certain peculiarities in the effects. Thus the various stimuli, which might cause, through an ordinary sensitive nerve, the sense of pain, would, if applied to the optic nerve, cause a sensation as of flashes of light; if applied to the olfactory, there would be a sense as of something smelt. And so with the other two.

Hence the explanation of so-called *subjective* sensations. Irritation in the optic nerve, or the part of the brain from which it arises, may cause a patient to believe he sees flashes of light, and among the commonest troubles of the nerves of special sense, is the distressing noise in the head (*tinnitus aurium*), which depends on some unknown stimulation of the auditory nerve or centre quite unconnected with external sounds.

Conduction in Motor Nerves.—Conduction in motor nerves presents a remarkable contrast with the foregoing. Thus—the effect of applying a stimulus to the motor nerve is always noticeable, at the peripheral extremity, in the contraction of muscles supplied by it. If a motor nerve be severed, irritation of the distal portion causes contraction of muscle, but no effect whatever is produced by stimulating that part of the nerve which is still in direct connection with the nerve-centre.

Contractions are excited in all the muscles supplied by the branches given off by the nerve below the point irritated, and in those muscles alone: the muscles supplied by the branches which come off from the nerve at a higher point than that irritated, are not directly excited to contraction. And it is from the same fact that, when a motor nerve enters a plexus and contributes with other nerves to the formation of a nervous trunk proceeding from the plexus, it does not impart motor power to the whole of that trunk, but only retains it isolated in the fibres which form its continuation in the branches of that trunk.

Functions of Nerve-Centres.

The functions of nerve-centres may be classified as follows:— 1. *Conduction.* 2. *Transference.* 3. *Reflection.* 4. *Automatism.* 5. *Augmentation.* 6. *Inhibition.*

1. **Conduction.**—Conduction in or through nerve-centres may be thus simply illustrated. The food in a given portion of the intestines, acting as a stimulus, produces a certain impression on the nerves in the mucous membrane, which impression is conveyed through them to the adjacent ganglia of the sympathetic. In ordinary cases, the consequence of such an impression on the ganglia is the movement by reflex action (p. 560) of the muscular coat of that and the adjacent part of the canal. But if irritant substances be mingled with the food, the sharper stimulus produces a stronger impression, and this is *conducted through* the nearest ganglia to others more and more distant; and, from all these, reflex motor impulses issuing, excite a wide-extended and more forcible action of the intestines. Or even through the sympathetic ganglia, the impression may be further conducted to the ganglia of the spinal nerves, and through them to the spinal cord, whence may issue motor impulses to the abdominal and other muscles, producing cramp. And yet further, the same morbid impression may be conducted through the spinal cord to the brain, where it may be *felt.* In the opposite direction, mental influence may be conducted from the brain through a succession of nervous centres—the spinal cord and ganglia, and one or more ganglia of the sympathetic—to produce the influence of the mind on the digestive and other organs; altering both the quantity and quality of their secretions.

2. **Transference.**—It has been previously stated that impressions conveyed by any centripetal nerve-fibre travel uninterruptedly throughout its whole length, and are not communicated to adjacent fibres.

When such an impression, however, reaches a nerve-centre, it may seem to be communicated to another fibre or fibres; as pain or some other kind of sensation may be felt in a part different altogether from that from which, so to speak, the stimulus started. Thus, in disease of the hip, there may be pain in the knee. This apparent change of place of a sensation to a part to which it would not seem properly to belong is termed transference.

The transference of impressions may be illustrated by the fact just referred to,—the pain in the knee, which is a common sign of disease of the hip. In this case the impression made by the disease on the nerves of the hip-joint is conveyed to the spinal cord ; there it is *transferred* to the central ends or connections of the nerve-fibres which are distributed about the knee. Through these the transferred impression is conducted to the brain, which, referring the sensation to the part from which it usually through these fibres receives impressions, feels as if the disease and the source of pain were in the knee. At the same time that it is transferred, the *primary* impression may be also conducted to the brain ; and in this case the pain is felt in both the hip and the knee. And so, in whatever part of the respiratory organs an irritation may be seated, the impression it produces, being conducted to the medulla oblongata, is transferred to the central connections of the nerves of the larynx ; and thence, being conducted as in the last case to the brain, the latter perceives the peculiar sensation of tickling in the glottis, which excites the act of coughing. Or, again, when the sun's light falls strongly on the eye, a tickling may be felt in the nose, exciting sneezing.

A variety of transference, which may be termed radiation of impressions, is shown when an impression received by a nervous centre is diffused to many other parts in the same centre, and produces sensations extending far beyond the part from which the primary impression was derived. Hence, as in the former cases, result various kinds of what have been denominated sympathetic sensations. Sometimes such sensations are referred to almost every part of the body : as in the shock and tingling of the skin produced by some startling noise. Sometimes only the parts immediately surrounding the point first irritated participate in the effects of the irritation ; thus, the aching of a tooth may be accompanied by pain in the adjoining teeth, and in all the surrounding parts of the face ; the explanation of such a case being, that the irritation conveyed to the brain by the nerve-fibres of the diseased tooth is *radiated* to the central ends of adjoining fibres, and that the mind perceives this secondary impression as if it were derived from the peripheral ends of the fibres.

3. **Reflection.**—In the cases of transference of nerve-force just described, it has been said that all that need be assumed is a com-

munication of the excited condition of an afferent nerve to other parts of its nerve-centre than that from which it takes its origin. In the case of *reflection*, on the other hand, the stimulus having been conveyed to a nerve-centre by a centripetal nerve, is conducted away again by a centrifugal nerve, and effects some change —motor, secretory or nutritive, at the peripheral extremity of the latter—the difference in effect depending on the variety of centrifugal nerve secondarily affected. As in transference, the reflection may take place from a certain limited set of centripetal nerves to a corresponding and related set of centrifugal nerves ; as when in consequence of the impression of light on the retina, the iris contracts, but no other muscle moves. Or the reflection may extend to widely different parts : as when an irritation in the larynx brings all the muscles engaged in expiration into coincident movement. Reflex movements, occurring quite independently of sensation, are generally called *excito-motor* ; those which are guided or accompanied by sensation, but not to the extent of a distinct perception or intellectual process are termed *sensori-motor*.

Laws of reflex action.—(*a*) For the manifestation of every reflex action, these things are necessary : (1), one or more perfect *centripetal* nerve-fibres, to convey an impression ; (2), a *nervous centre* for its reception, and by which it may be reflected ; (3), one or more *centrifugal* nerve-fibres, along which the impression may be conducted to (4), the muscular or other tissue by which the effect is manifested (p. 554). In the absence of any one of these conditions, a proper reflex action could not take place ; and whenever, for example, impressions made by external stimuli on sensory nerves give rise to motions, these are never the result of the direct reaction of the sensory and motor fibres of the nerves on each other ; in all such cases the impression is conveyed by the afferent fibres to a nerve-centre, and is therein communicated to the motor fibres.

(*b*) All reflex actions are essentially involuntary, though most of them admit of being modified, controlled, or prevented by a voluntary effort.

(*c*) Reflex actions performed in health have, for the most part, a distinct purpose, and are adapted to secure some end desirable for the well-being of the body ; but, in disease, many of them are irregular and purposeless. As an illustration of the first point, may be mentioned movements of the digestive canal, the respiratory movements, and the contraction of the eyelids and the pupil to exclude many rays of light, when the retina is exposed to a bright glare. These and all other normal reflex acts afford also examples of the mode in which the nervous centres *combine* and arrange co-ordinately the actions of the nerve-fibres, so that many muscles may act together for the common end. Another instance of the same kind furnished by the spasmodic contractions of the glottis on the contact of carbonic acid, or any foreign substance, with the surface of the epiglottis or larynx. Examples of the purposeless irregular nature of morbid reflex action are seen in the convulsive movements of epilepsy, and in the spasms of tetanus and hydrophobia.

(*d*) Reflex muscular acts are often more sustained than those produced by the direct stimulus of muscular nerves. The irritation of a muscular organ, or its motor nerve, produces contraction lasting only so long as the irritation continues; but irritation applied to a nervous centre through one of its centripetal nerves, may excite reflex and harmonious contractions, which last some time after the withdrawal of the stimulus (Volkmann).

Classification of Reflex Actions.—Reflex actions may be classified as follows (Kuss):—1. Those in which both the centripetal and centrifugal nerves concerned are *cerebro-spinal; e.g.*, deglutition, sneezing, coughing, and, in pathological conditions, tetanus, epilepsy. 2. Those in which the centripetal nerve is *cerebro-spinal*, and the centrifugal is *sympathetic*, most often *vaso-motor; e.g.*, secretion of saliva, or gastric juice; blushing or pallor of the skin. 3. Those in which the centripetal nerve is of the *sympathetic* system, and the centrifugal is *cerebro-spinal.* The majority of these are pathological, as in the case of convulsions produced by intestinal worms, or hysterical convulsions. 4. Those in which both centripetal and centrifugal nerves are of the *sympathetic* system: as, for example, the obscure actions which preside over the secretion of the intestinal fluids, those which unite the various generative functions and many pathological phenomena.

Relations between the Stimulus and the Resulting Reflex Action.—Certain rules showing the relation between the resulting reflex action and the stimulus have been drawn up by Pflüger, as follows:—

1. *Law of unilateral reflection.*—A slight irritation of sensory nerves is reflected along the motor nerves of the same region. Thus, if the skin of a frog's foot be tickled on the *right* side, the *right* leg is drawn up.

2. *Law of symmetrical reflection.*—A stronger irritation is reflected, not only on one side, but also along the corresponding motor nerves of the opposite side. Thus, if the spinal cord of a man has been severed by a stab in the back, when one foot is tickled *both* legs will be drawn up.

3. *Law of intensity.*—In the above case, the contractions will be more violent on the side irritated.

4. *Law of radiation.*—If the irritation (afferent impulse) increases, it is reflected along the motor nerves which spring from points higher up the spinal cord, till at length all the muscles of the body are thrown into action.

Simple and Co-ordinated Reflex Actions.—In the simplest form of reflex action a single nerve cell with an afferent and an efferent fibre is concerned, but in the majority of actual actions a number of cells are probably concerned, and the impression is as it were distributed among them, and they act in concert or co-ordination. This co-ordinating power belongs to nerve centres.

Primary and Secondary or acquired reflex actions.—We must carefully distinguish between such reflex actions which may be termed *primary*, and those which are *secondary* or *acquired.* As examples, of the former class we may cite sucking, contraction of the pupil, drawing up the legs when the toes are tickled, and many others which are performed as perfectly by the infant as by the adult.

The large class of *secondary* reflex actions consists of acts which require for their first performance and many subsequent repetitions an effort of will, but which by constant repetition are habitually though not necessarily performed, mechanically, *i.e.*, without the intervention of consciousness and volition. As instances we may take reading, writing, walking, &c.

In endeavouring to conceive how such complicated actions can be performed without consciousness and will, we must suppose that in the first instance the will directs the nerve-force along certain channels causing the performance of certain acts, *e.g.*, the various movements of flexion and extension involved in walking. After a time by constant repetition, these routes become, to use a metaphor, well *worn:* there is, as it were, a beaten track along which the nerve-force travels with much greater ease than formerly: so much so that a slight stimulus such as the pressure of the foot on the ground, is sufficient to start and keep going indefinitely the complex reflex actions of walking during entire mental abstraction, or even during sleep. In such acts as reading, writing, and the like, it would appear as if the will set the necessary reflex machinery going, and that the reflex actions go on uninterruptedly until again interfered with by the will.

Without this capacity possessed by the nervous system of "organising conscious actions into more or less unconscious ones," education or training would be impossible. A most important part of the process by which these acquired reflex actions come to be performed automatically consists in what is termed *association.* If two acts be at first performed voluntarily in succession, and this succession is often repeated, the performance of the first is at once followed mechanically by the second. Instances of this "force of habit" must be within the daily experience of every one.

Of course it is only such actions as have become entirely reflex that can be performed during complete unconsciousness, as in sleep. Cases of somnambulism are of course familiar to every one, and authentic instances are on record of persons writing and even playing the piano during sleep.

4. **Automatism.**—To nerve centres, it is said, belongs the property of originating nerve-impulses, as well as of receiving them and conducting and reflecting them.

The term *automatism* is employed to indicate the origination of nervous impulses in nerve-centres, and their conduction therefrom, independently of previous reception of a stimulus from another part. It is impossible, in the present state of our knowledge, to say definitely what actions in the body are really in this sense automatic. An example of automatic nerve-action has been already referred to, *i.e.*, that of the respiratory centre, but the apparently best examples of automatism are found, however, in the case of the cerebrum, which will be presently considered.

5. and 6. **Augmentation and Inhibition.**—Nerve cells not only receive and reflect nerve impulses, and also in some cases even originate such impulses, but they are also capable of increasing the impulse, and the result is what is called *augmentation*; and

when a nerve centre is in action its action is also capable of being increased or diminished (*inhibition*) by afferent impulses. This is the case in whatever way the centre has caused the action, whether of itself or by means of previous afferent impulses. The action, by which a centre is capable of being inhibited or exalted, has been well shewn in the case of the vaso-motor centre, before described (p. 193). This power, which can be exerted from the periphery, is very important in regulating the action even of partially automatic centres such as the respiratory centre.

Cerebro-spinal Nervous System.

The physiology of the cerebro-spinal nervous system includes that of the Spinal Cord, Medulla Oblongata, and Brain, of the several Nerves given off from each, and of the Ganglia on those nerves.

Membranes of the Brain and Spinal Cord.—The Brain and Spinal Cord are enveloped in three membranes—(1) the Dura Mater, (2) the Arachnoid, (3) the Pia Mater.

(1.) The *Dura Mater*, or external covering, is a tough membrane composed of bundles of connective tissue which cross at various angles, and in whose interstices branched connective-tissue corpuscles lie : it is lined by a thin elastic membrane, and on the inner surface, and, where it is not adherent to the bone, on the outer surface also is a layer of endothelial cells very similar to those found in serous membranes. (2.) The *Arachnoid* is a much more delicate membrane very similar in structure to the dura mater, and lined on its outer or free surface by an endothelial membrane. (3.) The *Pia Mater* consists of two chief layers, between which numerous blood-vessels ramify. Between the arachnoid and pia mater is a network of fibrous-tissue trabeculæ sheathed with endothelial cells : these sub-arachnoid trabeculæ divide up the sub-arachnoid space into a number of irregular sinuses. There are some similar trabeculæ, but much fewer in number, traversing the sub-dural space, *i.e.*, the space between the dura mater and arachnoid.

"*Pacchionian* bodies" are growths from the sub-arachnoid network of connective-tissue trabeculæ which project through small holes in the inner layers of the dura mater into the venous sinuses of that membrane. The venous sinuses of the dura mater have been injected from the sub-arachnoidal space through the intermediation of these villous outgrowths known as "*Pacchionian* bodies.'

The Spinal Cord and its Nerves.

The Spinal cord is a cylindriform column of nerve-substance connected above with the brain through the medium of the medulla oblongata, and terminating below, about the lower border of the first lumbar vertebra, in a slender filament of grey substance, the *filum terminale*, which lies in the midst of the roots of many nerves forming the *cauda equina*.

Structure.— The cord is composed of white and grey nervous substance, of which the former is situated externally, and constitutes its chief portion, while the latter occupies its central or axial portion, and is so arranged, that on

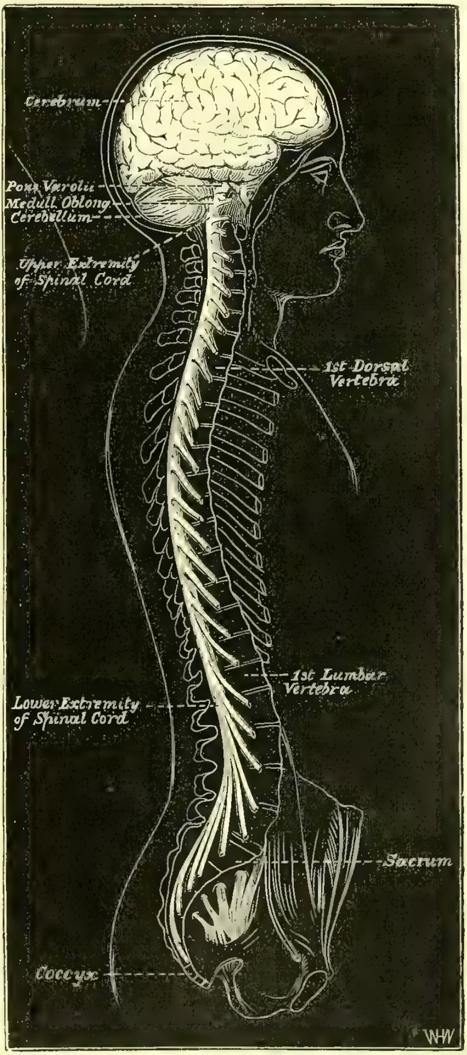


Fig. 315.—*View of the cerebro-spinal axis of the nervous system.* The right half of the cranium and trunk of the body has been removed by a vertical section; the membranes of the brain and spinal marrow have also been removed, and the roots and first part of the fifth and ninth cranial, and of all the spinal nerves of the right side, have been dissected out and laid separately on the wall of the skull and on the several vertebræ opposite to the place of their natural exit from the cranio-spinal cavity. (After Bourgery.)

the surface of a transverse section of the cord it appears like two somewhat crescentic masses connected together by a narrower portion or isthmus (fig. 318). Passing through the centre of this isthmus in a longitudinal direction is a minute canal (central canal), which is continued through the whole length of the cord, and opens above into the space at the back of medulla oblongata and pons Varolii, called the fourth ventricle. It is lined by a layer of columnar ciliated epithelium.

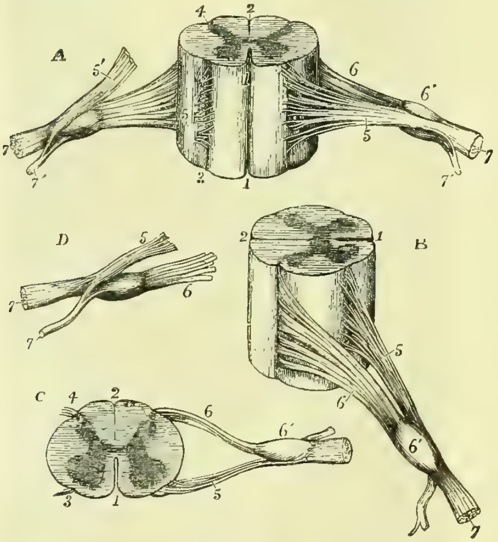


Fig. 316.—*Different views of a portion of the spinal cord from the cervical region; with the roots of the nerves* (slightly enlarged). In A, the anterior surface of the specimen is shown; the anterior nerve-root of its right side being divided; in B, a view of the right side is given; in C, the upper surface is shown; in D, the nerve-roots and ganglion are shown from below. 1. The anterior median fissure; 2, posterior median fissure; 3, anterior lateral depression, over which the anterior nerve-roots are seen to spread; 4, posterior lateral groove, into which the posterior roots are seen to sink; 5, anterior roots passing the ganglion; 5′, in A, the anterior root divided; 6, the posterior roots, the fibres of which pass into the ganglion 6′; 7, the united or compound nerve; 7′, the posterior primary branch, seen in A and D to be derived in part from the anterior and in part from the posterior root. (Allen Thomson).

The spinal cord consists of two exactly symmetrical halves separated anteriorly and posteriorly by vertical *fissures* (the posterior fissure being deeper, but less wide and distinct than the anterior), and united in the middle by nervous matter which is usually described as forming two commissures—an *anterior* commissure, in front of the central canal, consisting of medullated nerve fibres, and a *posterior* commissure behind the central canal consisting also of medullated nerve-fibres, but with more neuroglia, which gives the grey aspect to this commissure (fig. 316, B). Each half of the spinal cord is marked on the sides (obscurely at the lower part, but distinctly above) by two longitudinal furrows, which divide it into three portions, columns, or tracts, an *anterior*, *lateral*, and *posterior*. From the groove between the anterior and lateral columns spring the *anterior roots* of the spinal nerves (B and C, 5); and just in front of the groove between the lateral and posterior column arise the *posterior roots* of the same (B, 6): a pair of roots on each side corresponding to each vertebra (fig. 317).

White matter.—The white matter of the cord is made up of medullated nerve fibres, of various sizes, arranged longitudinally around the cord under the pia mater and passing in to support the individual fibres in the delicate connective tissue or *neuroglia* made up of a very fine reticulum, with both small cells almost filled up by nuclei and stellate, branching corpuscles.

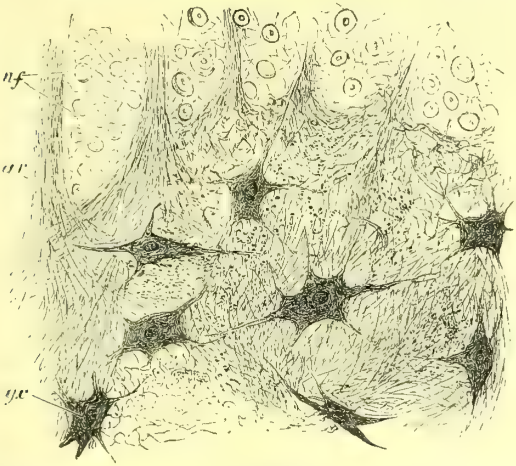


Fig. 317.—*Section of grey matter of anterior cornu of a calf's spinal cord; n f*, nerve-fibres of white matter in transverse section, showing axis-cylinder in centre of each; *a r*, anterior roots of spinal nerve passing out through white matter; *g c*, large stellate nerve-cells with nuclei; they are seen imbedded in neuroglia. (Schofield.)

Size.—The general rule respecting the size of different parts of the cord appears to be, that the size of each part bears a direct proportion to the size and number of nerve-roots given off from itself, and has but little relation to the size or number of those given off below it. Thus the cord is very large in the middle and lower part of its cervical portion, whence arise the large nerve-roots for the formation of the brachial plexuses and the supply of the upper extremities, and again enlarges at the lowest part of its dorsal portion and the upper part of its lumbar, at the origins of the large nerves which, after forming the lumbar and sacral plexuses, are distributed to the lower extremities. The chief cause of the greater size at these parts of the spinal cord is increase in the quantity of grey matter ; for there seems reason to believe that the white or fibrous part of the cord becomes gradually and progressively larger from below upwards, doubtless from the addition of a certain number of upward passing fibres from each pair of nerves.

From careful estimates of the number of nerve-fibres in a transverse section of the cord towards its upper end, and the number entering it by the anterior and posterior roots of each pair of nerves, it has been shown that in the human spinal cord not more than half of the total number of nerve-fibres entering the cord through all the spinal nerves are contained in a transverse section near its upper end. It is obvious, therefore, that at least half of the nerve-fibres entering it must terminate in the cord itself.

Grey matter.—The grey matter of the cord consists essentially of an extremely delicate network of the primitive fibrillæ of axis-cylinders, and which are derived from the ramification of multipolar ganglion cells of very large size, containing large round nuclei with nucleoli. This fine plexus is called *Gerlach's network*, and is mingled with the meshes of neuroglia, which in some parts is chiefly fibrillated, in others mainly granular and punctiform. The neuroglia is prolonged from the surface into the tip of the posterior cornu of grey matter and forms a jelly-like transparent substance, which when hardened is found to be reticular, and is called the *substantia gelatinosa* of Rolando.

The multipolar cells are either scattered singly or arranged in groups, of which the following are to be distinguished :—(*a*) In the *anterior cornu.* The groups found in the anterior cornu are generally two—one at the lateral part near the lateral column, and the other at the tip of the cornu in the middle line—sometimes, as in the lumbar enlargement, there is a third group more posterior. The cells of the anterior group are the largest. Into many of these cells the fibres of the anterior motor nerve-roots can be distinctly traced. (*b.*) In the *tractus intermedio-lateralis.* A group of nerve-cells midway between the anterior and posterior cornua, near the external surface of the grey matter. It is especially developed in the dorsal and also in the upper cervical region. (*c.*) In the *posterior vesicular columns* of Lockhart Clarke. These are found in the posterior cornua of grey matter towards the inner surface, extending from the cervical enlargement to the third lumbar nerves (fig. 318, *c*). (*d.*) Smaller cells are scattered throughout the grey matter, but are found chiefly at the tip (caput cornu) of the posterior cornu, in a finely granular basis, and among the posterior root fibres (*substantia gelatinosa cinerea* of Rolando).

The nerve-cells are connected by their processes immediately with the axis-cylinders of the fibres of the anterior or motor nerve-roots: whereas the nerve-cells of the posterior roots are connected with nerve-fibres, not directly, but only through the intermediation of Gerlach's nerve-network, in which their branching processes lose themselves.

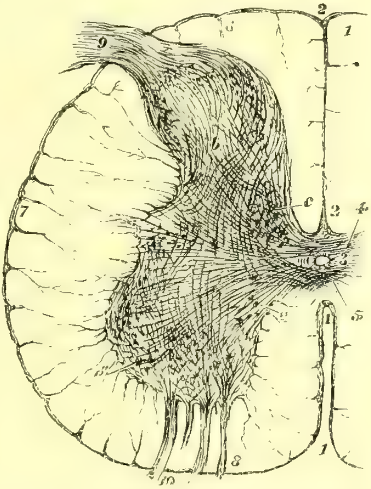


Fig. 318.—*Transverse section of half the spinal cord in the lumbar enlargement* (semi-diagrammatic). 1. Anterior median fissure; 2, posterior median fissure; 3, central canal lined with epithelium; 4, posterior commissure; 5, anterior commissure; 6, posterior column; 7, lateral column; 8, anterior column. The white substance is traversed by radiating trabeculæ of pia mater. 9, Fasiculus of posterior nerve-root entering in one bundle; 10, fasciculi of anterior roots entering in four spreading bundles of fibres; *b*, in the cervix cornu, decussating fibres from the nerve-roots and posterior commissure; *c*, posterior vesicular columns of Lockhart Clarke. About half way between the central canal and 7 are seen the group of nerve-cells forming the tractus intermedio-lateralis; *e*, *e*, fibres of anterior roots; *e'*, fibres of anterior roots which decussate in anterior commissure. (Allen Thomson.) × 6.

Spinal Nerves.—The spinal nerves consist of thirty-one pairs, issuing from the sides of the whole length of the cord, their number corresponding with the intervertebral foramina through which they pass. Each nerve arises by two roots, an anterior and posterior, the latter being the larger. The roots emerge through separate apertures of the sheath of dura mater surrounding the cord; and directly after their emergence, where the roots lie in the intervertebral foramen, a ganglion is found on the posterior root. The anterior root lies in contact with the anterior surface of the ganglion, but none of its fibres intermingle with those in the ganglion (5, fig. 316). But immediately beyond the ganglion the two roots coalesce, and by the mingling of their fibres form a compound or mixed spinal nerve, which, after issuing from the intervertebral canal, divides into an anterior and posterior branch, each containing fibres from both the roots (fig. 316).

The anterior root of each spinal nerve arises by numerous separate and converging bundles from the anterior column of the cord; the posterior root by more numerous parallel bundles, from the posterior column, or, rather, from the posterior part of the lateral column (fig. 318), for if a fissure be directed inwards from the groove between the middle and posterior columns, the posterior roots will remain attached to the former. The anterior roots of each spinal nerve consist of *centrifugal* fibres; the posterior as exclusively of *centripetal* fibres.

Course of the Fibres of the Spinal Nerves.—(*a*) The *Anterior roots* enter the cord in several bundles which may be called:—(1) Internal; (2) Middle; (3) External; all being more or less connected with the groups of multipolar cells in the anterior cornua. 1. The *internal* fibres are partly connected with internal group of nerve cells of anterior cornu of the same side; but some fibres pass over, through anterior commissure to end in the anterior cornu of opposite side, probably in internal group of cells. 2. The *middle* fibres are partly in connection with the lateral group of cells in anterior cornu, and in part, pass backwards to posterior cornu, having no connection with cells. 3. The *external* fibres are partly in connection with the lateral group of cells in the anterior cornu, but some fibres proceed direct into the lateral column without connection with cells and pass upwards in it.

(*b*) The *Posterior roots* enter the posterior cornua in two chief bundles, either at the tip, through or round the substantia gelatinosa, or by the inner side. The former enter the grey matter at once, and as a rule, turn upwards or downwards for a certain distance and then pass horizontally, some fibres reach the anterior cornua, passing at once horizontally; and the others, the opposite side, through the posterior grey commissure. Of those which enter by the inner side of the cornua the majority pass up (or down) in the white substance of the posterior columns, and enter the grey matter at various heights at the base of the posterior cornu, perhaps some pass directly upwards without entering the grey matter. Those that enter the grey matter pass in various directions, some to join the lateral cells in the anterior cornu, some join the cells in the posterior vesicular column, and some pass across to the other side of the cord in the anterior commissure, whilst others become again longitudinal in the grey matter.

It should be here mentioned that the cells in the posterior vesicular column are connected with medullated fibres which pass horizontally to the white matter of the lateral columns and there become longitudinal.

Course of the fibres in the cord. The nerve fibres which form the white matter of the cord are nearly all longitudinal fibres. It is, however, a matter of great difficulty to trace these fibres by mere dissection, and so some other methods must be adopted. One method is based upon the fact that nerve fibres undergo degeneration when they are cut off from the centre with which they are connected, or when the parts to which they are distributed are removed, as in amputation of a limb; and information as to the course of the fibres has been obtained by tracing the course of these degenerated tracts. The second method consists in observing the development of the various tracts; some have their medullary substance later than others, and are to be distinguished by their more grey appearance. The chief tracts which have been made out are the following:—

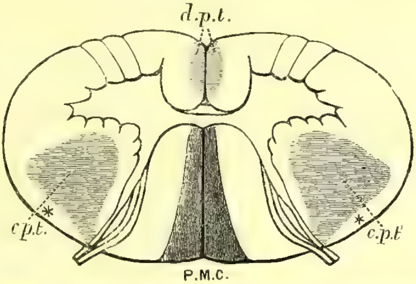


Fig. 319.—*Diagram of the spinal cord at the lower cervical region* to show the track of fibres; *d. p. t.*, direct pyramidal tract; *c. p. t.*, crossed pyramidal tract; * direct cerebellar tract; P. M. C., posterior medium column. (Gowers.)

(1) *The direct pyramidal tract* (fig. 319 *d.p.t.*), a comparatively small portion of the inner part of the anterior columns, which is traceable from the anterior pyramids of the medulla to the mid-dorsal region of the spinal cord. It consists of the fibres of the pyramids which do not undergo decussation in the medulla. There is reason for believing, however, that these fibres of the

direct pyramidal tract undergo decussation throughout their course, and fibres pass over through the anterior commissure to join the lateral pyramidal tract (*vide infra*); (2) the *Crossed pyramidal tract* (fig. 319, *c.p.t.*) can be traced from the anterior pyramids of the medulla, and consists of fibres which decussate in the anterior fissure and pass downwards in the lateral columns near the posterior cornu of the grey matter to the lower end of the cord; (3) *Direct cerebellar tract* (fig. 319), which corresponds to the peripheral portion of the posterior lateral column between the crossed pyramidal tract and the edge of the cord, can be traced up directly to the cerebellum and down to the mid-lumbar region; (4) *Posterior medium column*, or *Fasciculus of Goll*, is found on either side of the posterior commissure, and is traceable upwards as the fasciculus gracilis of the medulla, the fibres are connected with the cells of the posterior vesicular column. It is traceable downwards to the mid-dorsal region. As regards the remaining part of the cord unoccupied by the above tracts little can be said. The portion of the posterior column between the posterior median column and the posterior roots of the spinal nerves, known as *fasciculus cuneatus* or *Burdach's column*, is composed of fibres of the posterior roots on their way to enter the grey substance at different heights. The antero-lateral column contains fibres from the anterior cornua of the same as well as of the opposite side.

Functions of the Spinal Nerves.—The anterior spinal nerve-roots are efferent or motor: the posterior are afferent or sensory (Sir C. Bell). The fact is proved in various ways. Division of the anterior roots of one or more nerves is followed by complete loss of motion in the parts supplied by the fibres of such roots; but the sensation of the same parts remains perfect. Division of the posterior roots destroys the sensibility of the parts supplied by their fibres, while the power of motion continues unimpaired. Moreover, irritation of the ends of the distal portions of the divided anterior roots of a nerve excites muscular movements; irritation of the ends of the proximal portions, which are still in connection of the cord, is followed by no appreciable effect. Irritation of the distal portions of the divided posterior roots, on the other hand, produces no muscular movements and no manifestations of pain; for, as already stated, sensory nerves convey impressions only towards the nervous centres: but irritation of the proximal portions of these roots elicits signs of intense suffering. Occasionally, under this last irritation, muscular movements also ensue; but these are either voluntary, or the result of the irritation being reflected from the sensory to the motor fibres. Occasionally, too, irritation of the distal ends of divided anterior roots elicits signs of pain, as well as producing muscular movements: the pain thus excited is probably the result either of *cramp* or of so-called recurrent sensibility (Brown-Séquard).

Recurrent Sensibility.—If the anterior root of a spinal nerve be divided and the peripheral end be irritated, not only movements of the muscles supplied by the nerve take place, but also of other muscles, indicative of pain. If the main trunk of the nerve (after the coalescence of the roots beyond the ganglion) be divided, and the anterior root be irritated as before, the general signs of pain still remain, although the contraction of the muscles does not occur. The signs of pain disappear when the posterior root is divided. From these experiments it is believed that the stimulus passes down the anterior root to the mixed nerve and returns to the central nervous system through the posterior root by means of certain sensory fibres from the posterior root, which loop back into the anterior root, before continuing their course into the mixed nerve-trunk.

Functions of the Ganglia on Posterior Roots.—The ganglia act as centres for the nutrition of the nerves, since when the nerves are severed from connection with the ganglia, the parts of the nerves so severed degenerate, whilst the parts which remain in connection with them do not.

Functions of the Spinal Cord.

The power of the spinal cord, as a nerve-centre, may be arranged under the heads of (1) Conduction; (2) Transference; (3) Reflex action.

(1) *Conduction.*—The functions of the spinal cord in relation to *conduction*, may be best remembered by considering its anatomical connections with other parts of the body. From these it is evident that, with the exception of some few filaments of the sympathetic, there is no way by which nerve-impulses can be conveyed from the trunk and extremities to the brain or *vice versâ*, other than that

formed by the spinal cord. Through it, the impressions made upon the peripheral extremities or other parts of the spinal sensory nerves are conducted to the brain, where alone they can be *perceived.* Through it, also, the stimulus of the will, conducted from the brain, is capable of exciting the action of the muscles supplied from it with motor nerves. And for all these conductions of impressions to and fro between the brain and the spinal nerves, the perfect state of the cord is necessary; for when any part of it is destroyed, and its communication with the brain is interrupted, impressions on the sensory nerves given off from it below the seat of injury, cease to be propagated to the brain, and the brain loses the power of voluntarily exciting the motor nerves proceeding from the portion of cord isolated from it. Illustrations of this are furnished by various examples of paralysis, but by none better than by the common paraplegia, or loss of sensation and voluntary motion in the lower part of the body, in consequence of destructive disease or injury of a portion, including the whole thickness, of the spinal cord. Such lesions destroy the communication between the brain and all parts of the spinal cord below the seat of injury, and consequently cut off from their connection with the brain the various organs supplied with nerves issuing from those parts of the cord.

It is probable that the conduction of impressions along the cord is effected (at least, for the most part) through the grey substance, *i.e.*, through the nerve-corpuscles and filaments connecting them. But all parts of the cord are not alike able to conduct all impressions; and as there are separate nerve-fibres for motor and for sensory impressions, so in the cord, separate and determinate parts serve to conduct always the same kind of impression.

Experiments (chiefly by Brown-Séquard), point to the following conclusions regarding the conduction of sensory and motor impressions through the spinal cord.

It is important to bear in mind that the *grey* matter of the cord, though it conducts impressions giving rise to sensation, appears not to be sensitive when it is directly stimulated. The explanation probably is, that it possesses no apparatus such as exists at the peripheral terminations of sensory nerves, for the reception of sensory impressions.

a. Sensory impressions, conveyed to the spinal cord by root fibres of the posterior nerves are not conducted to the brain only by the posterior columns of the cord, but pass through them in great part into the central grey substance, by which they are transmitted to the brain (*p r*, fig. 320).

b. The impressions thus conveyed to the grey substance do not pass up to the brain to more than a slight degree, along that half of the cord corresponding to the side from which they have been received, but cross over to the other side almost immediately after entering the cord, and along it are transmitted to the brain. There is thus, in the cord itself, an almost complete decussation of sensory impressions brought to it; so that division or disease of one posterior half of the cord (3, fig. 320) is followed by loss of sensation, not in parts on the corresponding, but in those of the opposite side of the body. From the same fact it happens that a

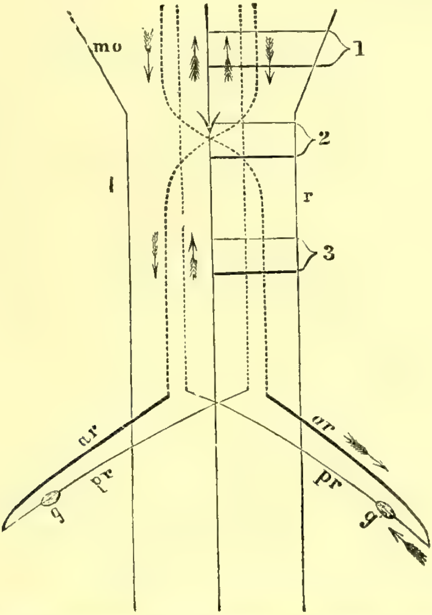


Fig. 320.—*Diagram of the decussation of the conductors for voluntary movements, and those for sensation:* **a, r, anterior roots and their continuations in the spinal cord, and decussation at the lower part of the medulla oblongata, *m o*; *p r*, the posterior roots and their continuation and decussation in the spinal cord; *g g*, the ganglions of the roots. The arrows indicate the direction of the nervous action; *r*, the right side; *l*, the left side. 1, 2, 3, indicate places of alteration in a lateral half of the spino-cerebral axis, to show the influence on the two kinds of conductors, resulting from section of the cord at any one of these three places. (After Brown-Séquard.)**

longitudinal antero-posterior section of the cord, along its whole length most completely abolishes sensibility on both sides of the body.

c. The various sensations of touch, pain, temperature, and muscular contraction, are probably conducted along separate and distinct sets of fibres. All, however, with the exception of the last named, undergo decussation in the spinal cord.

d. The posterior columns of the cord appear to have a great share in reflex movements.

e. Impulses of the will, leading to voluntary contractions of muscles, appear to be transmitted principally along the antero-lateral columns; but if a transverse section of this part be made (the grey matter being intact) although at first no voluntary movements of the part below occur, this paralysis is only temporary indicating that the grey matter may take on the conduction of these impulses.

f. Decussation of motor impulses occurs, not in the spinal cord, as is the case with sensory impressions, but at the anterior part of the medulla oblongata (fig. 321). Hence, motor impulses, having made their decussation, first enter the cord by the lateral tracts and adjoining grey matter, and then pass to the anterior columns and to the grey matter associated with them. Accordingly, division of the anterior pyramids, at the point of decussation (2, fig. 320), is followed by paralysis of motion in all parts below; while division of the olivary bodies which constitute the true continuations of the anterior columns of the cord, appears to produce very little paralysis. Disease or division of any part of the cerebro-spinal axis above the seat of decussation (1, fig. 320) is followed, as well-known, by impaired or lost power of motion on the opposite side of the body; while a like injury inflicted below this part (3, fig. 320), induces similar paralysis on the corresponding side.

When one half of the spinal cord is cut through, complete anæsthesia of the other side of the body below the point of section results, but there is often greatly increased sensibility (hyperæsthesia) on the same side; so much so that the least touch appears to be agonising. This condition may persist for several days. Similar effects may, in man, be the result of injury. Thus, in a patient who had sustained a severe lesion of the spinal cord in the cervical region, causing extensive paralysis and loss of sensation in the lower half of the body, there were two circumscribed areas, one on each arm, symmetrically placed, in which the gentlest touch caused extreme pain.

In addition to the transmission of ordinary sensory and motor impulses, the spinal cord is the medium of conduction also of impulses to and from the *vaso-motor centre* in the medulla oblongata, and probably also contains special vaso-motor centres.

2. **Transference.**—Examples of the transference of impressions in the cord have been given (p. 558); and that the transference takes place in the cord, and not in the brain, is nearly proved by the frequent cases of pain felt in the knee and not in the hip, in diseases of the hip; of pain felt in the urethra or glans penis, and not in the bladder, in calculus; for, if both the primary and the secondary or transferred impression were in the brain, both should be felt.

3. **Reflection.**—In man the spinal cord is so much under the control of the higher nerve-centres, that its own individual functions in relation to reflex action are apt to be overlooked; so that the result of injury, by which the cord is cut off completely from the influence of the encephalon, is apt to lessen rather than increase our estimate of its importance and individual endowments Thus, when the human spinal cord is divided, the lower extremities fall into any position that their weight and the resistance of surrounding objects combine to give them; if the body is irritated, they do not move towards the irritation; and if they are touched, the consequent reflex movements are disorderly and purposeless; all power of voluntary movement is absolutely abolished. In other mammals, *e.g.*, rabbit or dog, after recovery from the shock of the operation, which takes some time, reflex actions in the parts below will occur after the spinal cord has been divided, a very feeble irritation being followed by extensive and co-ordinate movements. In the case of the frog, however, and many other cold-blooded animals, in which experimental and other injuries of the nerve tissues are better borne, and in which the lower nerve-centres are less subordinate in their action to the higher, the reflex functions of the cord are still more clearly shown. When, for example, a frog's head is cut off, the limbs remain in, or assume a natural position; they resume it when disturbed; and when the abdomen or back is irritated, the feet are moved with the manifest purpose

of pushing away the irritation. The main difference in the cold-blooded animals being that the reflex movements are more definite, complicated, and effective, although less energetic than in the case of mammals. It is as if the mind of the animal were still engaged in the acts; and yet all analogy would lead us to the belief that the spinal cord of the frog has no different endowment, in *kind*, from those which belong to the cord of the higher vertebrata: the difference is only in *degree*. And if this be granted, it may be assumed that, in man and the higher animals, many actions are performed as reflex movements occurring through and by means of the spinal cord, although the latter cannot by itself initiate or even direct them independently.

Co-ordinate Movement not a proof of Consciousness.—The evident adaptation and purpose in the movements of the cold-blooded animals, have led some to think that they must be conscious and capable of will without their brains. But purposive movements are no proof of consciousness or will in the creature manifesting them. The movements of the limbs of headless frogs are not more purposive than the movements of our own respiratory muscles are; in which we know that neither will nor consciousness is at all times concerned. It may not, indeed, be assumed that the acts of standing, leaping, and other movements, which decapitated cold-blooded animals can perform, are also always, in the entire and healthy state, performed involuntarily, and under the sole influence of the cord; but it is probable that such acts may be, and commonly are, so performed, the higher nerve-centres of the animal having only the same kind of influence in modifying and directing them, that those of man have in modifying and directing the the movements of the respiratory muscles.

Inhibition of Reflex Actions.—The fact that such movements as are produced by iritating the skin of the lower extremities in the human subject, after division or disorganisation of a part of the spinal cord, do not follow the same irritation when the mind is active and connected with the cord through the brain, is, probably, due to the mind ordinarily perceiving the irritation and instantly controlling the muscles of the irritated and other parts; for, even when the cord is perfect, such involuntary movements will often follow irritation, if it be applied when the mind is wholly occupied. When, for example, one is anxiously thinking, even slight stimuli will produce involuntary and reflex movements. So, also, during sleep, such reflex movements may be observed, when the skin is touched or tickled; for example, when one touches with the finger the palm of the hand of a sleeping child, the finger is grasped—the impression on the skin of the palm producing a reflex movement of the muscles which close the hand. But when the child is awake, no such effect is produced by a similar touch.

Further, many reflex actions are capable of being more or less controlled or even altogether prevented by the will: thus an *inhibitory* action may be exercised by the brain over reflex functions of the cord and the other nerve centres. The following may be quoted as familiar examples of this inhibitory action:—

To prevent the reflex action of crying out when in pain, it is often sufficient firmly to clench the teeth or to grasp some object and hold it tight. When the feet are tickled we can, by an effort of will, prevent the reflex action of jerking them up. So, too, the involuntary closing of the eyes and starting, when a blow is aimed at the head, can be similarly restrained.

Darwin has mentioned an interesting example of the way in which, on the other hand, such an instinctive reflex act may override the strongest effort of the will. He placed his face close against the glass of the cobra's cage in the Reptile House at the Zoological Gardens, and though, of course, thoroughly convinced of his perfect security, could not by any effort of the will prevent himself from starting back when the snake struck with fury at the glass.

It has been found by experiment that in a frog the optic lobes and optic thalami have a distinct action in inhibiting or delaying reflex action, and also that more generally any afferent stimulus, if sufficiently strong, may *inhibit* or *modify* any reflex action even in the absence of these centres.

On the whole, therefore, it may, from these and like facts, be concluded that reflex acts, performed under the influence of the reflecting power of the spinal cord, are essentially independent of the brain and may be performed perfectly when the brain is separated from the cord: that these include a much larger number of the natural and purposive movements of the lower animals than of the warm-blooded animals and man: and that over nearly all of them the mind may exercise, through the higher nerve centres, some control; *determining*, *directing*, *hindering*, or *modifying*, them, either by direct action, or by its power over associated muscles.

To these instances of spinal reflex action, some add yet many more, including nearly all the acts which seem to be performed unconsciously, such as those of walking, running, writing, and the like: for these are really involuntary acts. It is true that at their first performances they are voluntary, that they require education for their perfection, and are at all times so constantly performed in obedience to a mandate of the will, that it is difficult to believe in their essentially involuntary nature. But the will really has only a *controlling* power over their performance; it can hasten or stay them, but it has little or nothing to do with the actual carrying out of the effect. And this is proved by the circumstance that these acts can be performed with complete mental abstraction: and, more than this, that the endeavour to carry them out entirely by the exercise of the will is not only not beneficial, but positively interferes with their harmonious and perfect performance. Anyone may convince himself of this fact by trying to take each step as a voluntary act in walking down stairs, or to form each letter or word in writing by a distinct exercise of the will.

These actions, however, will be again referred to, when treating of their possible connection with the functions of the so-called *sensory ganglia*, p. 593 *et seq.*

Morbid reflex actions.—The relation of the reflex action to the strength of the stimulus is the same as was shewn generally in the action of ganglia, a slight stimulus producing a slight (p. 562) movement and a greater, a greater movement, and so on; but in instances, in which we must assume that the cord is *morbidly more irritable*, *i.e.*, apt to issue more nervous force than is proportionate to the stimulus applied to it, a slight impression on a sensory nerve produces extensive reflex movements. This appears to be the condition in tetanus, in which a slight touch on the skin may throw the whole body into convulsion. A similar state is induced by the introduction of strychnia, and, in frogs, of opium, into the blood; and numerous experiments on frogs thus made tetanic, have shown that the tetanus is wholly unconnected with the brain, and depends on the state induced in the spinal cord.

Special Centres in Spinal Cord.—It may seem to have been implied that the spinal cord, as a single nerve-centre, reflects alike from all parts all the impressions conducted to it. But it is more probable that it should be regarded as a collection of nervous centres united in a continuous column. This is made probable by the fact that segments of the cord may act as distinct nerve-centres, and excite motions in the parts supplied with nerves given off from them; as well as by the analogy of certain cases in which the muscular movements of single organs are under the control of certain circumscribed portions of the cord. Thus,—for the governance of the sphincter-muscles concerned in guarding the orifices respectively of the rectum and urinary bladder there are special nerve-centres in the lower part of the spinal cord (*ano-spinal* and *vesico-spinal* centres); while the actions of these are temporarily *inhibited* by stimuli which lead to defæcation and micturition. So also, there are centres directly concerned in erection of the penis and in the emission of semen (*genito-urinary*). The *emission of semen* is a reflex act: the irritation of the glans penis conducted to the spinal cord, and thence reflected, excites the successive and co-ordinate contractions of the muscular fibres of the vasa deferentia and vesiculæ seminales, and of the accelerator urinæ and other muscles of the urethra; and a forcible expulsion of semen takes place, over which the mind has little or no control, and which, in cases of paraplegia, may be unfelt. *The erection of the penis*, also, as already explained (p. 211), appears to be in part the result of a reflex contraction of the muscles by which the veins returning the blood from the penis are compressed. The involuntary *action of the uterus in expelling its contents during parturition*, is also of a purely reflex kind, dependent in part upon the spinal cord, though in part also upon the sympathetic system: its independence of the brain being proved by cases of delivery in paraplegic women, and also by the fact that delivery can take place whilst the patient is under the influence of chloroform. But all these spinal nerve-centres are intimately connected, both structurally and physiologically, one with another, as well as with those higher encephalic centres, without whose guiding influence their actions may become disorderly and purposeless, or altogether abrogated.

Centre for Movements of Lymphatic Hearts of Frog.—Volkmann has shown that the rhythmical movements of the anterior pair of lymphatic hearts in the frog depend upon nervous influence derived from the portion of spinal cord corresponding to the third vertebra, and those of the posterior pair on influence supplied by the portion of cord opposite the eighth vertebra. The movements of the heart continue, though the whole of the cord, except the above portions, be destroyed; but on the instant of destroying either of these portions, though all the rest of the cord be untouched, the movements of the corresponding hearts cease. What appears to be thus proved in regard to two portions of the cord, may be inferred to prevail in other portions also; and the inference is reconcilable with most of the facts known concerning the physiology and comparative anatomy of the cord.

Tone of Muscles.—The influence of the spinal cord on the sphincter ani (centre for *defæcation*) has been already mentioned (see above). It maintains this muscle in permanent contraction, so that, except in the act of defæcation, the orifice of the anus is always closed. This influence of the cord resembles its common reflex action in being involuntary, although the will can act on the muscle to make it contract more, or may inhibit the action of the ano-spinal centre so as to permit its dilatation. The condition of the sphincter ani, however, is not altogether exceptional. It is the same in kind, though it exceeds in degree that condition of muscles which has been called *tone*, or passive contraction; a state in which they always when not active appear to be during health, and in which, though called inactive, they are in slight contraction, and certainly are not relaxed, as they are long after death, or when the spinal cord is destroyed. This tone of all the muscles of the trunk and limbs depends on the spinal cord, as the contraction of the sphincter ani does. If an animal be killed by injury or removal of the brain the tone of the muscles may be felt and the limbs feel firm as during sleep; but if the spinal cord be destroyed, the sphincter ani relaxes, and all the muscles feel loose, and flabby, and atonic, and remain so till *rigor mortis* commences. This kind of tone must be distinguished from that mere firmness and tension which it is customary to ascribe, under the name of *tone*, to all tissues that feel robust and not flabby, as well as to muscles. The tone peculiar to muscles has in it a degree of vital contraction: that of other tissues is only due to their being well nourished, and therefore compact and tense.

All the foregoing examples illustrate the fact that the spinal cord is a collection of reflex centres, upon which the higher centres act by sending down impulses to set in motion, to modify or to control them. The movements or other phenomena of reflection being as it were the function of the ganglion cells to set in action, after an afferent impression has been conveyed to them by the posterior nerve-trunks in connection with them. The extent of the resulting movement depends upon the strength of the stimulus, the position at which it was applied as well as upon the condition of the nerve cells; the connection between the cells being so intimate that a series of co-ordinated movements may result from a single stimulation, first of all affecting one cell. Whether the cells possess as well the power of originating impulses (automatism) is doubtful, but this is possible in the case of *vaso-motor centres* which are situated in the cord (p. 192), and of *sweating centres* which must be closely related to them, and possibly in the case of the centres for maintaining the *tone of muscles.*

The Medulla Oblongata.

The medulla oblongata (figs. 321, 322), is a column of grey and white nervous substance formed by the prolongation upwards of the spinal cord and connecting it with the brain.

Structure.—The grey substance which it contains is situated in the interior and variously divided into masses and laminæ by the white or fibrous substance which is arranged partly in external columns, and partly in fasciculi traversing the central grey matter. The medulla oblongata is larger than any part of the spinal cord. Its columns are pyriform, enlarging as they proceed towards the brain, and are continuous with those of the spinal cord. Each half of the medulla, therefore, may be divided into three columns or tracts of fibres, continuous with the three tracts of which each half of the spinal cord is made up. The columns are more prominent than those of the spinal cord, and separated from each other by deeper grooves. The *anterior*, continuous with the anterior columns

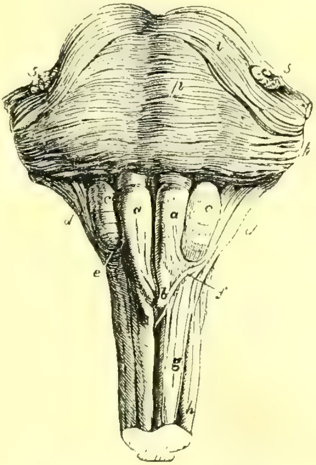


Fig. 321.—*Anterior surface of the pons Varolii, and medulla oblongata.* *a*, *a*, anterior pyramids; *b*, their decussation; *c*, *c*, olivary bodies; *d*, *d*, restiform bodies; *e*, arciform fibres; *f*, fibres described by Solly as passing from the anterior column of the cord to the cerebellum; *g*, anterior column of the spinal cord; *h*, lateral column; *p*, pons Varolii; *i*, its upper fibres; 5, 5, roots of the fifth pair of nerves.

of the cord, are called the anterior *pyramids;* the *posterior*, continuous with the posterior columns of the cord, and comprising the funiculus cuneatus, and the funiculus of Rolando (fig. 323, *f.c.*, *f.R.*), are called the *restiform* bodies. On the outer side of the anterior pyramids of each side, near its upper part, is a small oval mass containing grey matter, and named the *olivary body;* and at the posterior part of the restiform column, immediately on each side of the posterior median groove, continuous with the posterior median column of the cord, a small tract is marked off by a slight groove from the remainder of the restiform body, and called the *posterior pyramid* or *fasciculus gracilis.* The restiform columns, instead of remaining parallel with each other throughout the whole length of the medulla oblongata, diverge near its upper part, and by thus diverging, lay open, so to speak, a space called the fourth ventricle, the floor of which is formed by the grey matter of the interior of the medulla, by this divergence exposed.

On separating the anterior pyramids, and looking into the groove between them, some decussating fibres of the lateral columns of the cord can be plainly seen.

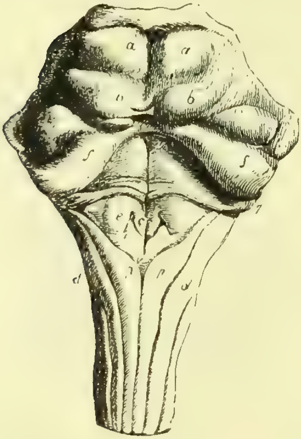


Fig. 322.—*Posterior surface of the pons Varolii, corpora quadrigemina, and medulla oblongata.* The peduncles of the cerebellum are cut short at the side. *a*, *a*, the upper pair of corpora quadrigemina; *b*, *b*, the lower; *f*, *f*, superior peduncles of the cerebellum; *c*, eminence connected with the nucleus of the hypoglossal nerve; *e*, that of the glosso-pharyngeal nerve; *i*, that of the vagus nerve; *d*, *d*, restiform bodies; *p*, *p*, posterior pyramids; *v*, *v*, groove in the middle of the fourth ventricle, ending below in the calamus scriptorius; 7, 7, roots of the auditory nerves.

Distribution of the Fibres of the Medulla Oblongata.

The *anterior pyramid* of each side, although mainly composed of continuations of the fibres of the anterior columns of the spinal cord, receives fibres from the lateral columns, both of its own and the opposite side; the latter fibres forming almost entirely the decussating strands which are seen in the groove between the anterior pyramids. Thus composed, the anterior pyramidal fibres proceeding onwards to the brain are distributed in the following manner:—

1. The greater part pass on through the Pons to the Cerebrum. A portion of the fibres, however, running apart from the others, joins some fibres from the olivary body, and unites with them to form what is called the *olivary fasciculus* or *fillet*. 2. A small tract of fibres proceeds to the cerebellum.

The *lateral column* of the cord on each side of the medulla, in proceeding upwards, divides into three parts, outer, inner, and middle, which are thus disposed of :—1. The *outer* fibres (direct cerebellar tract) go with the restiform tract to the cerebellum. 2. The *middle* (crossed pyramidal tract) decussate across the middle line with their fellows, and form a part of the anterior pyramid of the opposite side. 3. The *inner* pass on to the cerebrum, at first superficially but afterwards beneath the olivary body and the arcuate fibres, and then proceed along the floor of the fourth ventricle, on each side, under the name of the *fasciculus teres.*

The posterior column of the cord is represented in the medulla by the *posterior pyramid*, or fasciculus gracilis, which is a continuation of the posterior median column, and by the *restiform body*, comprising the funiculus cuneatus and the funiculus of Rolando. The fasciculus gracilis (fig. 323, *f.g*), diverges above as the broader clava to form, one on either side, the lower lateral boundary of the fourth ventricle, then tapers off, and becomes no longer traceable. The funiculus cuneatus, or the rest of the posterior column of the cord, is continued up in the medulla as such (fig. 323, *f.c*) ; but soon, in addition, between this and the continuation of the posterior nerve roots, appears another tract called the funiculus of Rolando (fig. 323, *f.R*). High up, the funiculus cuneatus is covered by a set of fibres (arcuate fibres), which issue from the anterior median fissure, turn upwards over the anterior pyramids to pass directly into the corresponding hemisphere of the cerebellum, being joined by the fibres of the direct cerebellar tract ; the funiculus of Rolando, and the funiculus cuneatus, although appearing to join them, do not actually do so, except to a partial extent.

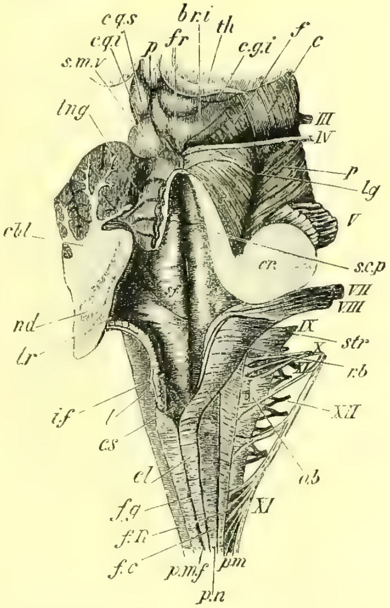


Fig. 323.—*Posterior view of the medulla, fourth ventricle, and mesencephalon* (natural size). *p. n*, line of the posterior roots of the spinal nerves; *p.m.f.*, posterior median fissure ; *f. g.*, funiculus gracilis ; *cl.*, its clavis ; *f.c.*, funiculus cuneatus ; *f.R.*, funiculus of Rolando ; *r.b.*, restiform body ; *c.s.*, calamus scriptorius ; *l*, section of ligula or tænia ; part of choroid plexus is seen beneath it ; *l.r.*, lateral recess of the ventricle ; *str.*, striæ acusticæ ; *i.f.*, inferior fossa ; *s.f.*, posterior fossa ; between it and the median sulcus is the fasciculus teres ; *cbl.*, cut surface of the cerebellar hemisphere ; *n.d.*, central or grey matter ; *s.m.v.*, superior medullary velum ; *lng.*, ligula ; *s.c.p.*, superior cerebellar peduncle cut longitudinally ; *cr.*, combined section of the three cerebellar peduncles ; *c.q.s.*, *c.q.i.*, corpora quadrigemina (superior and inferior) ; *fr.*, frænulum ; *f.*, fibres of the fillet seen on the surface of the tegmentum ; *c.*, crusti ; *l.g.*, lateral groove ; *c.g.i.*, corpus geniculum internus ; *th.*, posterior part of thalamus ; *p.*, pineal body. The roman numbers indicate the corresponding cranial nerves. (E. A. Schäfer.)

Grey matter of the medulla.—To a considerable extent the grey matter of the medulla is a continuation of that in the spinal cord, but the arrangement is somewhat different.

The displacement of the anterior cornu takes place because of the decussation of a large part of the fibres of the lateral columns in the anterior pyramids passing through the grey matter of the anterior cornu, so that the caput cornu is cut off from the rest of the grey matter, and is, moreover, pushed backwards by the olivary body, to be mentioned below. It lies in the lateral portion of the medulla, and exists for a time as the *nucleus lateralis* (fig. 324, *nl*); it consists of a reticulum of grey matter, containing ganglion cells intersected by white nerve fibres. The base of the anterior cornu is pushed more from the anterior surface, and when the central canal opens out into the fourth ventricle, forms a collection of ganglion cells, producing the eminence of the fasciculus teres; from certain large cells in it arise the hypoglossal nerve (fig. 325, *XII.*), which passes through the medulla, and appears between the olivary body and the anterior pyramids.

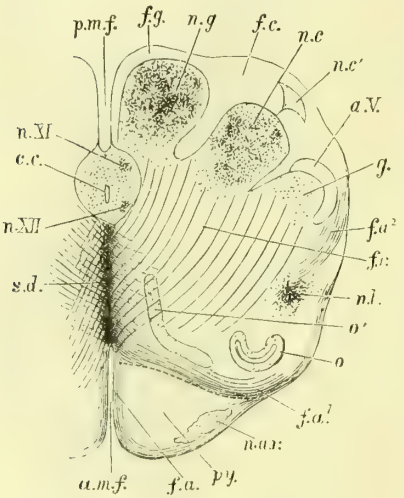


Fig. 324.—*Section of the medulla oblongata in the region of the superior pyramidal decussation.* *a.m.f.*, anterior median fissure; *f.a.*, superficial arciform fibres emerging from the fissure; *py.*, pyramid; *n.a.r.*, nuclei of arciform fibres; *f.a.*, deep arciform becoming superficial; *o.*, lower end of olivary nucleus; *n.l.*, nucleus lateralis; *f.r.*, formatio reticularis; *f.a.*², arciform fibres proceeding from the formatio reticularis; *g.*, substantia gelatinosa of Rolando; *a.V.*, ascending root of fifth nerve; *n.c.*, nucleus cuneatus; *n.c'.*, external cuneate nucleus; *n.g.*, nucleus gracilis; *f.g.*, nucleus gracilis; *p.m.f.*, posterior median fissure; *c.c.*, central canal surrounded by grey matter, in which are *n.XI.*, nucleus of the spinal accessory, and *n.XII.*, nucleus of the hypoglossal; *s.d.*, superior pyramidal decussation. (Schwalbe.) (Modified from Quain.)

In the funiculus teres, nearer to the middle line as well as to the surface, is a collection of nerve cells called the nucleus of that funiculus (fig. 325, *nt*). The grey matter of the posterior cornu is displaced somewhat by bands of fibres passing through it. The caput cornu appears at the surface as the funiculus of Rolando, whilst the cervix cornu is broken up into a reticulated structure which is displaced laterally, similar in structure to the nucleus lateralis. From the increase of the base of the posterior cornu, the nuclei of the funiculus gracilis and funiculus cuneatus are derived (fig. 324, *n.g.*, *n.c*), and outside of the latter is an accessory nucleus formed (fig. 324, *n.c'*). Internally to these latter, and also derived from the cells of the base of the posterior cornu and appearing in the floor of the fourth ventricle, when the central canal opens are the nuclei of the spinal accessory, vagus, and glosso-pharyngeal nerves. In the upper part of the medulla also, to the outside of these three nuclei, is found the principal auditory nucleus. All the above nuclei appear to be derived from a continuation of the grey matter of the spinal cord, but a fresh collection of grey matter not represented is interpolated between the anterior pyramids and the lateral column, contained within the olivary prominence, the wavy line of which (corpus dentatum) is doubled upon itself at an angle with the extremities directed upwards and inwards (fig. 325, *o*). There may also be a smaller collection of grey matter on the outer and inner side of the olivary nucleus known as accessory olivary nuclei.

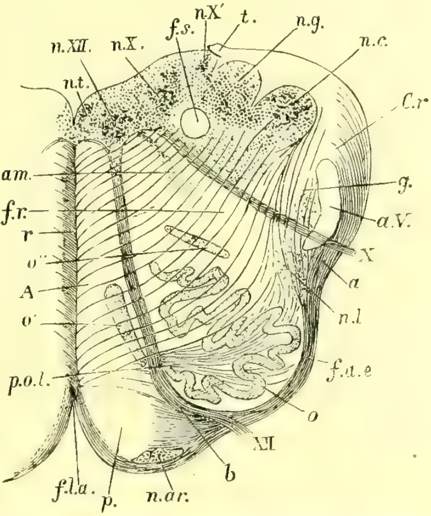


Fig. 325.—*Section of the medulla oblongata at about the middle of the olivary body.* *f.l.a.*, anterior median fissure; *n.ar.*, nucleus arciformis; *p.*, pyramid; *XII.*, bundle of hypoglossal nerve emerging from the surface; at *b*, it is seen coursing between the pyramid and the olivary nucleus, *o.*; *f.a.e.*, external arciform fibres; *n.l.*, nucleus lateralis; *a.*, arciform fibres passing towards restiform body, partly through the substantia gelatinosa, *g.*, partly superficial to the ascending root of the fifth nerve, *a.V.*; *X.*, bundle of vagus root emerging; *f.r.*, formatio reticularis; *c.r.*, corpus restiforme, beginning to be formed, chiefly by arciform fibres, superficial and deep; *n.c.*, nucleus cuneatus; *n.g.*, nucleus gracilis; *t*, attachment of the ligula; *f.s.*, funiculus solitarius; *n.X.*, *n.X.'*, two parts of the vagus nucleus; *n.XII.*, hypoglossal nucleus; *n.t.*, nucleus of the funiculus teres; *n.am.*, nucleus ambiguous; *r.*, raphe; *A.*, continuation of the anterior column of cord; *o'*, *o''*. accessory olivary nucleus; *p.o.*, pedunculus olivæ. (Schwalbe.) (Modified from Quain.)

Functions of the Medulla Oblongata.

The functions of the medulla oblongata, like those of the spinal cord, may be considered under the heads of: 1. Conduction; 2. Transference and Reflection; and, in addition, 3. Automatism.

1. In *conducting* impressions the medulla oblongata has a wider extent of function than any other part of the nervous system, since it is obvious that all impressions passing to and fro between the brain and the spinal cord and all nerves arising below the pons, must be transmitted through it.

2. As a nerve-centre by which impressions are *transferred* or *reflected*, the medulla oblongata also resembles the spinal cord;

the only difference between them consisting of the fact that many of the reflex actions performed by the former are much more important to life than any performed by the spinal cord.

Demonstration of Functions.—It has been proved by repeated experiments on the lower animals that the entire brain may be gradually cut away in successive portions, and yet life may continue for a considerable time, and the respiratory movements be uninterrupted. Life may also continue when the spinal cord is cut away in successive portions from below upwards as high as the point of origin of the phrenic nerve. In Amphibia, the brain has been all removed from above, and the cord, as far as the medulla oblongata, from below; and so long as the medulla oblongata was intact, respiration and life were maintained. But if, in any animal, the medulla oblongata is wounded, particularly if it is wounded in its central part, opposite the origin of the pneumogastric nerves, the respiratory movements cease, and the animal dies asphyxiated. And this effect ensues even when all parts of the nervous system, except the medulla oblongata, are left intact.

Injury and disease in men prove the same as these experiments on animals. Numerous instances are recorded in which injury to the medulla oblongata has produced instantaneous death; and, indeed, it is through injury of it, or of the part of the cord connecting it with the origin of the phrenic nerve, that death is commonly produced in fractures and diseases with sudden displacement of the upper cervical vertebræ.

Special Centres.

(1.) *Respiratory.*—The centre whence the nervous force for the production of combined respiratory movements appears to issue is in the interior of that part of the medulla oblongata from which the pneumogastric nerves or Vagi arise. The vagi themselves indeed, are not essential to the respiratory movements; for both may be divided without more immediate effect than a retardation of these movements. But in this part of the medulla oblongata is the nerve-centre whence the impulses producing the respiratory movements issue, and through which impulses conveyed from distant parts are reflected.

The wide extent of connection which belongs to the medulla oblongata as the centre of the respiratory movements, is shown by the fact that impressions by mechanical and other ordinary stimuli, made on many parts of the external or internal surface of the body, may modify, *i.e.*, increase or diminish the rapidity of respiratory movements. Thus involuntary respirations are induced by the sudden contact of cold with any part of the skin, as in dashing cold water on the face. Irritation of the mucous membrane of the nose produces sneezing. Irritation in the pharynx, œsophagus, stomach, or intestines, excites the concurrence of the respiratory movements to produce vomiting. Violent irritation in the rectum, bladder, or uterus, gives rise to a concurrent action of the respiratory muscles, so as to effect the expulsion of the fæces, urine, or fœtus.

(2) *Centre for Deglutition.*—The medulla oblongata appears to be the centre whence are derived the motor impulses enabling the muscles of the palate, pharynx, and œsophagus to produce the successive co-ordinate and adapted movements necessary to the act of *deglutition* (p. 296). This is proved by the persistence of swallowing in some of the lower animals after destruction of the cerebral hemispheres and cerebellum; its existence in anencephalous monsters; the power of swallowing possessed by the marsupial embryo before the brain is developed; and by the complete arrest of the power of swallowing when the medulla oblongata is injured in experiments. (3) A centre by which the movements of *mastication* are regulated (p. 279). (4) Through the medulla oblongata, chiefly, are reflected the impressions which excite the *secretion of saliva* (p. 286). (5) *Cardio-inhibitory* centre for the regulation of the action of the heart, through the pneumogastrics and probably also, the accelerating fibres of the sympathetic (p. 157). (6) The chief *vasomotor* centre. From this centre arise fibres which, passing down the spinal cord, issue with the anterior roots of the spinal nerves, and enter the ganglia and branches of the sympathetic system, by which they are conducted to the blood-vessels (p. 192). (7) *Cilio-spinal* centre for the regulation of the iris, and other plain-fibred muscles of the eye. (8 and 9) Centres or ganglia of the special senses of *hearing* and *taste*. (10) The centre for *speech*, *i.e.*, the centre by which the various muscular movements concerned in speech are co-ordinated or harmonised. (11) Centre by which the many muscles concerned in *vomiting* are har-

monised. (12) The so-called *diabetic* centre, or, in other words, the grey matter in the medulla oblongata which, being irritated, causes glycosuria (p. 351), is probably the vasomotor centre; and this peculiar result of its stimulation is merely due to vasomotor changes in the liver.

Though respiration and life continue while the medulla oblongata is perfect and in connection with the respiratory nerves, yet, when all the brain above it is removed, there is no more appearance of sensation, or will, or of any mental act in the animal, the subject of the experiment, than there is when only the spinal cord is left. The movements are all involuntary and unfelt; and the medulla oblongata has, therefore, no claim to be considered as an organ of the mind, or as the seat of sensation or voluntary power. These are connected with parts to be afterwards described.

Pons Varolii.

Structure.—The meso-cephalon, or pons Varolii (VI, fig. 326), is composed principally of tranverse fibres connecting the two hemispheres of the cerebellum, and forming its principal transverse commissure. But it includes, interlacing with these, numerous longitudinal fibres which connect the medulla oblongata with the cerebrum, and transverse fibres which connect it with the cerebellum. Among the fasciculi of nerve-fibres by which these several parts are connected, the pons also contains abundant grey or vesicular substance, which appears irregularly placed among the fibres, and fills up all the interstices.

Functions.—The anatomical distribution of the fibres, both transverse and longitudinal, of which the pons is composed, is sufficient evidence of its functions as a conductor of impressions from one part of the cerebro-spinal axis to another. Concerning its functions as a nerve-centre, little or nothing is certainly known.

Crura Cerebri.

Structure.—The *crura cerebri* (III, fig. 326), are principally formed of nerve-fibres, of which the inferior or more superficial (crusta) are continuous with those of the anterior pyramidal tracts of the medulla oblongata, and the superior or deeper fibres (tegmentum) with the lateral and posterior pyramidal tracts, and with the olivary fasciculus. Besides these fibres from the medulla oblongata, are others from the cerebellum; and some of the latter as well as a part of the fibres derived from the lateral tract of the medulla oblongata, decussate across the middle line.

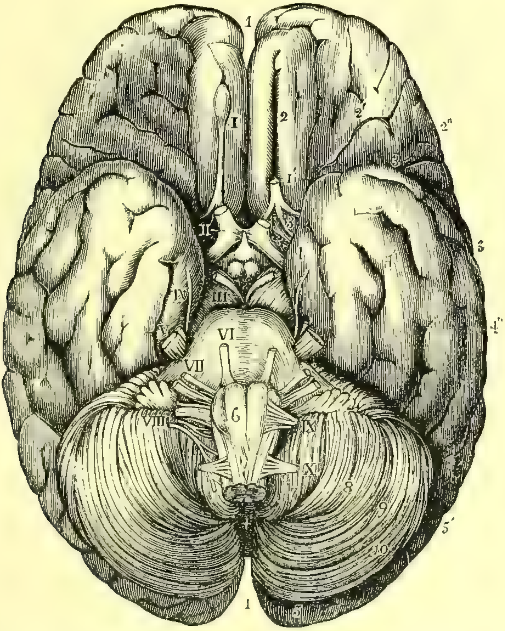


Fig. 326.—*Base of the brain.* 1, superior longitudinal fissure; 2, 2', 2'', anterior cerebral lobe; 3, fissure of Sylvius, between anterior and 4, 4', 4'', middle cerebral lobe; 5, 5', posterior lobe; 6, medulla oblongata; the figure is in the right anterior pyramid; 7, 8, 9, 10, the cerebellum; +, the inferior vermiform process. The figures from I. to IX. are placed against the corresponding cerebral nerves; III. is placed on the right crus cerebri. VI. and VII. on the pons Varolii; X. the first cervical or suboccipital nerve. (Allen Thomson). $\frac{1}{2}$.

Each crus cerebri contains among its fibres a mass of grey substance, the *locus niger*.

Functions.—With regard to their functions, the crura cerebri may be regarded as, principally, conducting organs: the *crusta* conducting motor and the *tegmentum* sensory impressions. As nerve-centres they are probably connected with the functions of the third cerebral nerve, which arises from the *locus niger*, and through which are directed the chief of the numerous and complicated movements of the eyeball. The crura cerebri are also in all probability connected with the co-ordination of other movements besides those of the eye, as either rotatory (p. 599) or disorderly movements result after section of either of them.

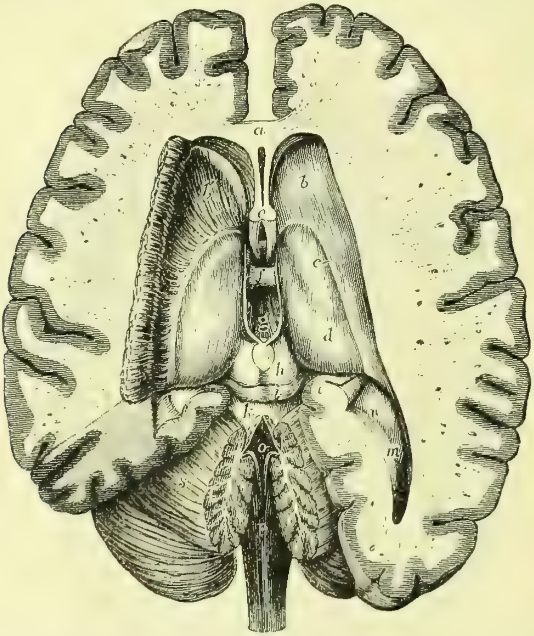


Fig. 327.—*Dissection of brain, from above, exposing the lateral fourth, and fifth ventricles with the surrounding parts.* ½.—*a*, anterior part, or *genu* of corpus callosum; *b*, corpus striatum; *b'*, the corpus striatum of left side, dissected so as to expose its grey substance; *c*, points by a line to the tænia semicircularis; *d*, optic thalamus; *e*, anterior pillars of fornix divided; below they are seen descending in front of the third ventricle, and between them is seen part of the anterior commissure; in front of the letter *e* is seen the slit-like fifth ventricle, between the two laminæ of the septum lucidum; *f*, soft or middle commissure; *g* is placed in the posterior part of the third ventricle; immediately behind the latter are the posterior commissure (just visible) and the pineal gland, the two crura of which extend forwards along the inner and upper margins of the optic thalami; *h* and *i*, the corpora quadrigemina; *k*, superior crus of cerebellum; close to *k* is the valve of Vieussens, which has been divided so as to expose the fourth ventricle; *l*, hippocampus major and corpus fimbriatum, or tænia hippocampi; *m*, hippocampus minor; *n*, eminentia collateralis; *o*, fourth ventricle; *p*, posterior surface of medulla oblongata; *r*, section of cerebellum; *s*, upper part of left hemisphere of cerebellum exposed by the removal of part of the posterior cerebral lobe. (Hirschfeld and Leveillé.)

Corpora Quadrigemina.

The corpora quadrigemina (from which, in function, the *corpora geniculata* are not distinguishable), are the homologues of the optic lobes in Birds, Amphibia, and Fishes, and may be regarded as the principal nerve-centres for the sense of sight.

Functions.—(1) The experiments of Flourens, Longet, and Hertwig, show that removal of the corpora quadrigemina wholly destroys the power of seeing; and diseases in which they are disorganised are usually accompanied by blindness. Atrophy of them is also often a consequence of atrophy of the eyes. Destruction of one of the corpora quadrigemina (or of one optic lobe in birds), produces blindness of the opposite eye. This loss of sight is the only apparent injury of sensibility sustained by the removal of the corpora quadrigemina. The (2) removal of one of them affects the movements of the body, so that animals rotate, as after division of the crus cerebri, only more slowly: but this may be due to giddiness and partial loss of sight. (3) The more evident and direct influence is that produced on the iris. It contracts when the corpora quadrigemina are irritated: it is always dilated when they are removed: so that they may be regarded, in some measure at least, as the nervous centres governing its movements, and adapting them to the impressions derived from the retina through the optic nerves and tracts. (4) The centre for the co-ordination of the movements of the eyes is also contained in them. This centre is closely associated with that for contraction of the pupil, and so it follows that contraction or dilatation follows upon certain definite ocular movements.

Corpora Striata and Optic Thalami.

Structure.—(1.) The corpora striata are situated in front of the optic thalami, partly within and partly without the lateral ventricle. Each corpus striatum consists of two parts.

(*a.*) Intraventricular portion (*caudate nucleus*) is conical in shape, with the base of the cone forwards; it consists of grey matter, with white substance in its centre, which comes from the corresponding cerebral peduncle. (*b.*) Extraventricular portion (*lenticular nucleus*) is separated from the other portion by a layer of white material. It is seen on section of the hemisphere. Its horizontal section is wider in the centre than at the end. On the outside is the grey lamina (*claustrum*).

Between the corpus striatum and optic thalamus is the *tænia* *semicircularis*, a semi-transparent band which is continued back into the white substance of the roof of the descending horn of the ventricle.

(2.) The Optic Thalami are oval in shape, and rest upon the crura cerebri. The upper surface of each thalamus is free, and of white substance, it projects into the lateral ventricle. The posterior surface is also white. The inner sides of the two optic thalami are in partial contact, and are composed of grey material uncovered by white, and are, as a rule, connected by a transverse portion.

Functions.—The two ganglia, the Corpus Striatum, and Optic Thalamus, are placed between the cerebral convolutions and the crus cerebri of the same side. It is probable that although some of the fibres of the crus pass without interruption into the cerebrum, the majority of the fibres pass into these ganglia first of all the lower fibres (crusta) into the corpus striatum, and the upper (tegmentum) into the optic thalamus, and then out into the cerebrum. From the position of these bodies, it would be reasonable to suppose that they were interposed in function between the operation of the will on the one hand, and on the other with the sensori-motor apparatus below them, and it is believed that this is the case, although the evidence is not exact : the theory that the corpus striatum is the *motor* ganglion, and that, when injured, the communication between the will and the muscles of one half of the body is broken (hemiplegia), being supported by many pathological facts and physiological experiments, and generally received by pathologists. It is found that the cerebral functions are as a rule unimpaired. In the same way the evidence that the optic thalamus is the *sensory* ganglion depends upon similar observations, that when injured or destroyed, sensation of the opposite side of the body is impaired or lost. In both cases, the parts paralysed are on the opposite side to the lesions, the decussation of both sets of fibres taking place, as we have seen, below the ganglia. It is a fact, however, that many experiments and pathological observations are opposed to the above theory, which must therefore be received with caution.

The Cerebellum.

The Cerebellum (7, 8, 9, 10, fig. 326), is composed of an elongated central portion called the vermiform processes, and two hemispheres. Each hemisphere is connected with its fellow, not only by means of the vermiform processes, but also by a bundle of fibres called the *middle crus* or *peduncle* (the latter forming the greater part of the pons Varolii), while the *superior crura* with the valve of Vieussens connect it with the cerebrum (5, fig. 328), and the *inferior crura* (formed by the prolonged restiform bodies) connect it with the medulla oblongata (3, fig. 328).

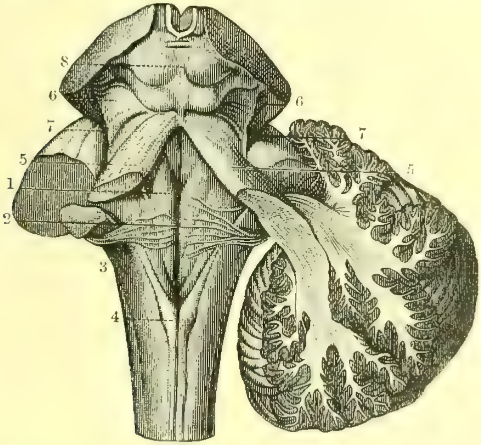


Fig. 328.—*Cerebellum in section and of fourth ventricle*, with the neighbouring parts. 1, median groove of fourth ventricle, ending below in the *calamus scriptorius*, with the longitudinal eminences formed by the *fasciculi teretes*, one on each side; 2, the same groove, at the place where the white streaks of the auditory nerve emerge from it to cross the floor of the ventricle; 3, inferior crus or peduncle of the cerebellum, formed by the restiform body; 4, posterior pyramid; above this is the calamus scriptorius; 5, superior crus of cerebellum, or processus e cerebello ad cerebrum (or ad testes); 6, 6, fillet to the side of the crura cerebri; 7, 7, lateral grooves of the crura cerebri; 8, corpora quadrigemina. (From Sappey after Hirschfeld and Leveillé).

Structure.—The cerebellum is composed of white and grey matter, the latter being external, like that of the cerebrum, and like it, infolded, so that a larger area may be contained in a given space. The convolutions of the grey matter, however, are arranged after a different pattern as shown in fig. 328. Besides the grey substance on the surface, there is, near the centre of the white substance of each hemisphere, a small capsule of grey matter called the *corpus dentatum* (fig. 329, *cd*), resembling very closely the *corpus dentatum* of the olivary body of the medulla oblongata (fig. 324, *o*).

If a section be taken through the cortical portion of the cerebellum, the following distinct layers can be seen (fig. 330) by microscopic examination.

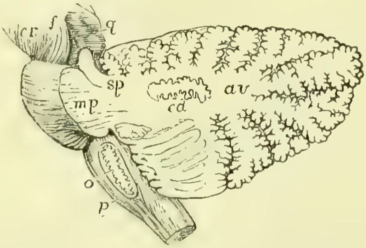


Fig. 329.—*Outline sketch of a section of the cerebellum, showing the corpus dentatum.* The section has been carried through the left lateral part of the pons, so as to divide the superior peduncle and pass nearly through the middle of the left cerebellar hemisphere. The olivary body has also been divided longitudinally so as to expose in section its *corpus dentatum.* *c r*, crus cerebri; *f*, fillet; *q*, corpora quadrigemina; *s p*, superior peduncle of the cerebellum divided; *m p*, middle peduncle or lateral part of the pons Varolii, with fibres passing from it into the white stem; *a v*, continuation of the white stem radiating towards the arbor vitæ of the folia; *c d*, corpus dentatum; *o*, olivary body with its corpus dentatum; *p*, anterior pyramid. (Allen Thomson). $\frac{2}{3}$.

(1.) Immediately beneath the pia mater (*p m*) is a layer of considerable thickness, which consists of a delicate connective tissue, in which are scattered several spherical corpuscles like those of the granular layer of the retina, and also an immense number of delicate fibres passing up towards the free surface and branching as they go. These fibres are the processes of the cells of Purkinje. (2.) *The Cells of Purkinje* (*p*). These are a single layer of branched nerve-cells, which give off a single unbranched process downwards, and numerous processes up into the external layer, some of which become continuous with the scattered corpuscles. (3.) *The granular layer* (*g*), consisting of immense numbers of corpuscles closely resembling those of the nuclear layers of the retina. (4.) *Nerve fibre layer* (*f*). Bundles of nerve-fibres forming the white matter of the cerebellum, which, from its branched appearance has been named the "arbor vitæ."

Functions.—The physiology of the Cerebellum may be considered in its relation to sensation, voluntary motion, and the instincts or higher faculties of the mind. Its supposed functions, like those of every other part of the nervous system, have been determined by physiological experiment, by pathological observation and by its comparative anatomy.

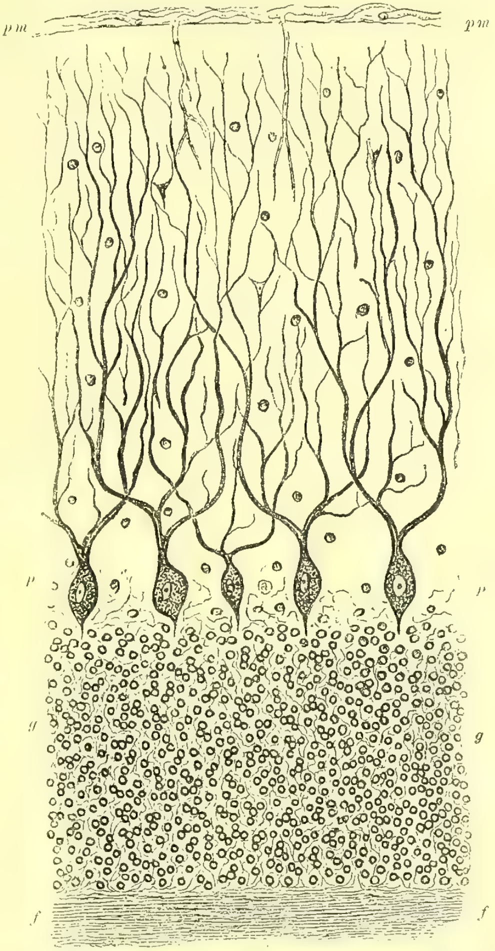


Fig. 330.—*Vertical section of dog's cerebellum ; p m*, pia mater ; *p*, corpuscles of Purkinje, which are branched nerve-cells lying in a single layer and sending single processes downwards and more numerous ones upwards, which branch continuously and extend through the deep "molecular layer" towards the free surface ; *g*, dense layer of ganglionic corpuscles, closely resembling nuclear layers of retina ; *f*, layer of nerve-fibres, with a few scattered ganglionic corpuscles. This last layer (*f f*) constitutes part of the *white* matter of the cerebellum, while the layers between it and the free surface are *grey* matter. (Klein and Noble Smith.)

(1.) *It is itself insensible to irritation*, and may be all cut away without eliciting signs of pain (Longet). Its removal or disorganization by disease is also generally unaccompanied by loss or disorder of sensibility ; animals from which it is removed can smell, see, hear, and feel pain, to all appearance, as perfectly as before (Flourens ; Magendie). Yet, if any of its crura be touched, pain is indicated ; and, if the restiform tracts of the medulla oblongata be irritated, the most acute suffering appears to be produced. So that, although the restiform tracts of the medulla oblongata, which themselves appear so sensitive, enter the cerebellum, it cannot be regarded as a principal organ of sensation.

(2.) *Co-ordination of Movements.*—In reference to motion, the experiments of Longet and many others agree that no irritation of the cerebellum produces movement of any kind. Remarkable results, however, are produced by removing parts of its substance. Flourens (whose experiments have been confirmed by those of Bouillaud, Longet, and others) extirpated the cerebellum in birds by successive layers. Feebleness and want of harmony of muscular movements were the consequence of removing the superficial layers. When he reached the middle layers, the animals became restless without being convulsed; their movements were violent and irregular, but their sight and hearing were perfect. By the time that the last portion of the organ was cut away, the animals had entirely lost the powers of springing, flying, walking, standing, and preserving their equilibrium. When an animal in this state was laid upon its back, it could not recover its former posture, but it fluttered its wings, and did not lie in a state of stupor; it saw the blow that threatened it, and endeavoured to avoid it. Volition and sensation, therefore, were not lost, but merely the faculty of combining the actions of the muscles; and the endeavours of the animal to maintain its balance were like those of a drunken man.

The experiments afforded the same results when repeated on all classes of animals; and from them and the others before referred to, Flourens inferred that the cerebellum belongs neither to the sensory nor the intellectual apparatus; and that it is not the source of voluntary movements, although it belongs to the motor apparatus; but is the organ for the co-ordination of the voluntary movements, or for the excitement of the *combined* action of muscles.

Such evidence as can be obtained from cases of disease of this organ confirms the view taken by Flourens; and, on the whole, it gains support from comparative anatomy; animals whose natural movements require most frequent and exact combinations of muscular actions being those whose cerebella are most developed in proportion to the spinal cord.

Foville supposed that the cerebellum is the organ of *muscular sense*, *i.e.*, the organ by which the mind acquires that knowledge of the actual state and position of the muscles which is essential to the exercise of the will upon them; and it must be admitted that all the facts just referred to are as well explained on this hypothesis as on that of the cerebellum being the organ for combining movements. A harmonious combination of muscular actions must depend as much on the capability of appreciating the condition of the muscles with regard to their tension, and to the force with which they are contracting, as on the power which any special nerve-centre may possess of exciting them to contraction. And it is because the power of such harmonious movement would be equally lost, whether the injury to the cerebellum involved injury to the seat of muscular sense, or to the centre for combining muscular actions, that experiments on the subject afford no proof in one direction more than the other.

The theory once believed, that the cerebellum is the organ of sexual passion, has been long disproved.

Forced Movements.—The influence of each half of the cerebellum is directed to muscles on the opposite side of the body; and it would appear that for the right ordering of movements, the actions of its two halves must be always mutually balanced and adjusted. For if one of its crura, or if the pons on either side of the middle line, be divided, so as to cut off from the medulla oblongata and spinal cord the influence of one of the hemispheres of the cerebellum, strangely disordered movements ensue (forced movements). The animals fall down on the side opposite to that on which the crus cerebelli has been divided, and then roll over continuously and repeatedly; the rotation being always round the long axis of their bodies, and generally from the side on which the injury has been inflicted. The rotations sometimes take place with much rapidity; as often, according to Magendie, as sixty times in a minute, and may last for several days. Similar movements have been observed in men; as by Serres in a man in whom there was apoplectic effusion in the right crus cerebelli; and by Belhomme in a woman, in whom an exostosis pressed on the left crus. They may, parhaps, be explained by assuming that the division or injury of the crus cerebelli produces paralysis or imperfect and disorderly movements of the opposite side of the body; the animal falls, and then, struggling with the disordered side on the ground, and striving to rise with the other, pushes itself over; and so again and again, with the same act, rotates itself. Such movements cease when the other crus cerebelli is divided; but probably only because the paralysis of the body is thus made almost complete. Other varieties of forced movements have been observed, especially those named "circus movements," when the animal operated upon moves round and round in a circle; and again those in which the animal turns over and over in a series of somersaults. Nearly all these movements may result on section of one or other of the following parts; viz. crura cerebri, medulla, pons, cerebellum, corpora quadrigemina, corpora striata, optic thalami, and even, it is said, of the cerebral hemispheres.

The Cerebrum.

The Cerebrum (composed of two so-called *Cerebral hemispheres*) is placed in connection with the Pons and Medulla oblongata by its two *crura* or *peduncles* (III. fig. 326): it is connected with the cerebellum by the processes called superior crura of the cerebellum, or *processus a cerebello ad testes*, and by a layer of grey matter, called the valve of Vieussens, which lies between these processes, and extends from the inferior vermiform process of the cerebellum to the corpora quadrigemina of the cerebrum. These parts, which thus connect the cerebrum with the other principal divisions of the cerebro-spinal system may, therefore, be regarded as the continuation of the cerebro-spinal axis or column; on which, as a kind of offset from the main nerve-path, the cerebellum is placed: and on the further continuation of which in the direct line, is placed the cerebrum (fig. 331).

The Cerebrum is constructed, like the other chief divisions of the cerebro-spinal system, of grey (vesicular and fibrous) and white (fibrous) matter; and, as in the case of the Cerebellum (and unlike the spinal cord and medulla oblongata), the grey matter (*cortex*) is external, and forms a capsule or covering for the white substance. For the evident purpose of increasing its amount without undue occupation of space, the grey matter is variously infolded so as to form the cerebral *convolutions*.

Convolutions of the Cerebrum.—For convenience of description, the surface of the brain has been divided into five lobes (Gratiolet).

1. *Frontal* (F. figs. 332, 333), limited behind by the fissure of Rolando (central fissure), and beneath by the fissure of Sylvius. Its surface consists of three main convolutions, which are approximately horizontal in direction and are broken up into numerous secondary gyri. They are termed the superior, middle, and inferior frontal convolutions. In addition, the frontal lobe contains, at its posterior part, a convolution which runs upwards almost vertically ("ascending frontal"), and is bounded in front by a fissure termed the præcentral, behind by that of Rolando.

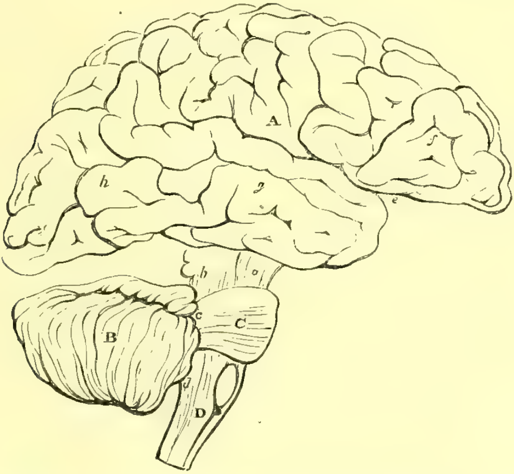


Fig. 331.—*Plan in outline of the encephalon*, as seen from the right side. ⅓. The parts are represented as separated from one another somewhat more than natural, so as to show their connections. A, cerebrum; *f*, *g*, *h*, its anterior, middle, and posterior lobes; *e*, fissure of Sylvius; B, cerebellum; C, pons Varolii; D, medulla oblongata; *a*, peduncles of the cerebrum; *b*, *c*, *d*, superior middle, and inferior peduncles of the cerebellum. (From Quain.)

2. *Parietal* (P.). This lobe is bounded in front by the fissure of Rolando, behind by the external perpendicular fissure (parieto-occipital), and below by the fissure of Sylvius. Behind the fissure of Rolando is the "ascending parietal" convolution, which swells out at its upper end into what is termed the superior parietal lobule. The superior parietal lobule is separated from the inferior parietal lobule by the intra-parietal sulcus. The inferior parietal lobule (pli courbe) is situated at the posterior and upper end of the fissure of Sylvius; it consists of (*a*) an anterior part (supra-marginal convolution) which hooks round the end of the fissure of Sylvius, and joins the superior temporal convolution, and a posterior part (*b*) (angular gyrus) which hooks round into the middle temporal convolution.

3. *Temporo-sphenoidal* (T.). contains three well-marked convolutions.

parallel to each other, termed the superior, middle, and inferior temporal. The superior and middle are separated by the parallel fissure.

4. *Occipital* (O.). This lobe lies behind the external perpendicular or parieto-occipital fissure, and contains three convolutions, termed the superior, middle, and inferior occipital. They are often not well marked. In man, the external parieto-occipital fissure is only to be distinguished as a notch in the inner edge of the hemisphere; below this it is quite obliterated by the four annectent gyri (plis de passage) which run nearly horizontally. The upper two connect the parietal, and the lower two the temporal with the occipital lobe.

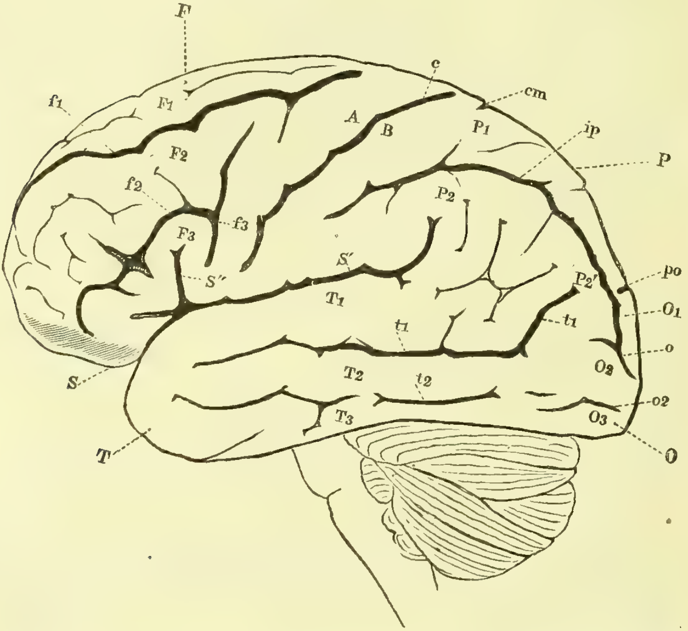


Fig. 332.—*Lateral view of the brain* (semi-diagrammatic). F, Frontal lobe; P, Parietal lobe; O, Occipital lobe; T, Temporo-sphenoidal lobe; S, fissure of Sylvius; S′, horizontal, S″, ascending ramus of the same; c, sulcus centralis (fissure of Rolando); A, ascending frontal; B, ascending parietal convolution; F_1, superior; F_2, middle; F_3, inferior frontal convolutions; f_1, superior, f_2, inferior frontal sulcus; f_3, præcentral sulcus; P_1, superior parietal lobule; P_2, inferior parietal lobule consisting of P_2, supramarginal gyrus, and P_2', angular gyrus; ip, interparietal sulcus; cm, termination of calloso-marginal fissure; O_1, first, O_2, second, O_3, third occipital convolutions; po, parieto-occipital fissure; o, transverse occipital fissure; o_2, sulcus occipitalis inferior; T_1, first, T_2, second, T_3, third temporo-sphenoidal convolutions; t_1, first, t_2, second temporo-sphenoidal fissures. (Ecker.)

5. The *central lobe*, or island of Reil, which contains a number of radiating convolutions (gyri operti).

The *internal* surface (fig. 334) contains the following gyri and sulci :

Gyrus fornicatus, a long curved convolution, parallel to and curving round the corpus callosum, and swelling out at its hinder and upper end into the quadrate lobule (præcuneus), which is continuous with the superior parietal lobule on the external surface.

Marginal convolution runs parallel to the preceding, and occupies the space between it and the edge of the longitudinal fissure.

The two convolutions are separated by the calloso-marginal fissure.

The *internal perpendicular* fissure is well marked, and runs downwards to its junction with the *calcarine* fissure : the wedge-shaped mass intervening between these two is termed the *cuneus*. The calcarine fissure corresponds to the projection into the posterior cornu of the lateral ventricle, termed the *Hippocampus minor*. The *temporo-sphenoidal lobe* on its internal aspect is seen to end in a hook (uncinate gyrus). The notch round which it curves is continued up and back as the dentate or hippocampal sulcus ; this fissure underlies the projection of the hippocampus major within the brain. There are three internal temporo-occipital convolutions, of which the superior and inferior ones are usually well marked, the middle one generally less so.

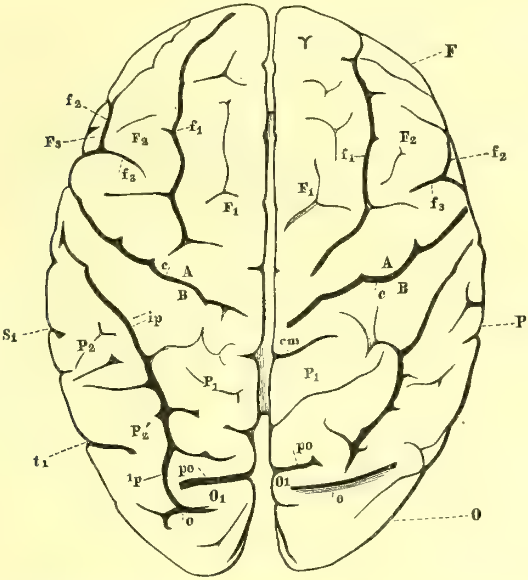


Fig. 333.—*View of the brain from above* (semi-diagrammatic). S1, end of horizontal ramus of fissure of Sylvius. The other letters refer to the same parts as in Fig. 332. (Ecker.)

The collateral fissure (corresponding to the eminentia collateralis) forms the lower boundary of the superior temporo-occipital convolution.

All the above details will be found indicated in the diagrams (figs. 332, 333, 334).

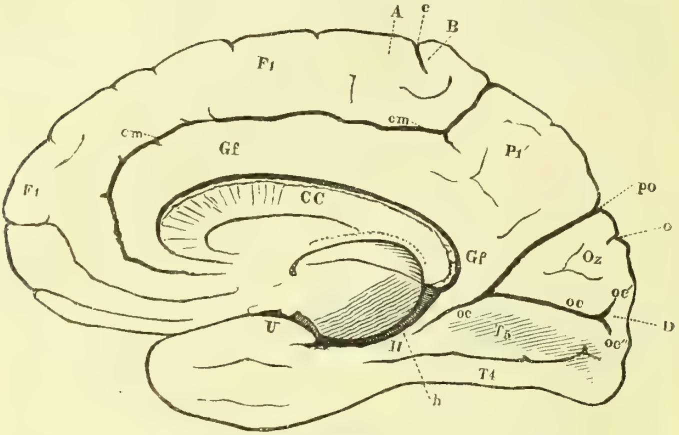


Fig. 334.—*View of the right hemisphere in the median aspect* (semi-diagrammatic). CC, corpus callosum longitudinally divided; Gf, gyrus fornicatus; H, gyrus hippocampi; h, sulcus hippocampi; U, uncinate gyrus; cm, calloso-marginal fissure; F1, median aspect of first frontal convolution; c, terminal portion of sulcus centralis (fissure of Rolando); A, ascending frontal; B, ascending parietal convolution; P1′, præcuneus; Oz, cuneus; po, parieto-occipital fissure; o, sulcus occipitalis transversus; oc, calcarine fissure; oc′, superior; oc″, inferior ramus of the same; D, gyrus descendens; T4, gyrus occipito-temporalis lateralis (lobulus fusiformis); T5, gyrus occipito-temporalis medialis (lobulus lingualis). (Ecker.)

Structure.—The cortical *grey matter* of the brain consists of five layers (Meynert) (fig. 335).

1. Superficial layer with abundance of neuroglia and a few small multipolar ganglion-cells. 2. A large number of closely packed small ganglion-cells of pyramidal shape. 3. The most important layer, and the thickest of all: it contains many large pyramidal ganglion-cells, each with a process running off from the apex vertically towards the free surface, and lateral processes at the base which are always branched. Also a median process from the base of each cell which is unbranched and becomes continuous with the axis-cylinder of a nerve-fibre. 4. Numerous ganglion-cells: termed the "granular formation" by Meynert. 5. Spindle-shaped and branched ganglion-cells of moderate-size arranged chiefly parallel to the free surface (vide fig. 335).

According to recent observations by Bousfield, the fibres of the medullary centre become connected with the multipolar ganglion cells of the fourth layer, and, from these latter, branches pass to the angles at the bases of the pyramidal cells of the third layer of the cortex (fig. 337, *a*). From the apices of the pyramidal cells, the axis-cylinder processes pass upwards for a considerable distance, and finally terminate in ovoid corpuscles (fig. 336) closely resembling, and homologous with, the corpuscles in which the ultimate ramifications of the branched cells of Purkinje in the cerebellum terminate. Thus it would seem that the large pyramidal cells of the third layer are themselves homologous with the cells of Purkinje in the cerebellum.

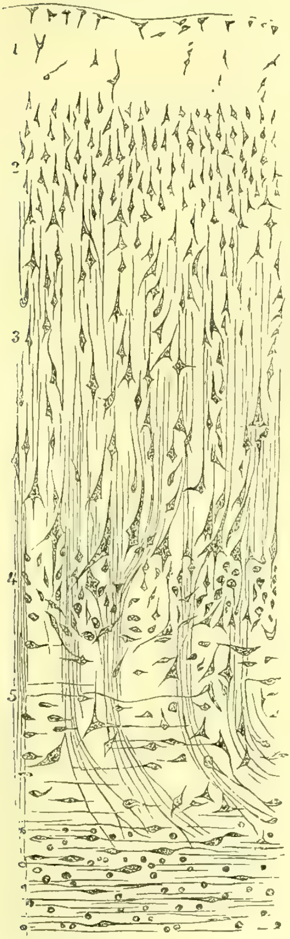


Fig. 335.—*The layers of the cortical grey matter of the cerebrum.* (Meynert.)

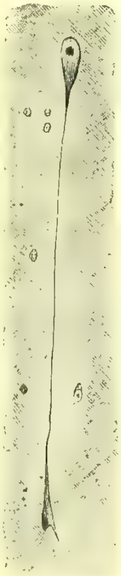


Fig. 336.

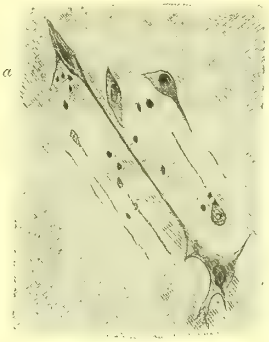


Fig. 337.—[Drawn by G. Munro Smith from ammonium bichromate preparations by E. C. Bousfield.]

The *white matter* of the brain, as of the spinal cord, consists of bundles of medullated, and, in the neighbourhood of the grey matter, of non-medullated nerve-fibres, which, however, as is the case in the central nervous system generally, have no external nucleated nerve-sheath, which are held together by delicate connective tissue. The size of the fibres of the brain is usually less than that of the fibres of the spinal cord : the average diameter of the former being about $\frac{1}{10,000}$ of an inch.

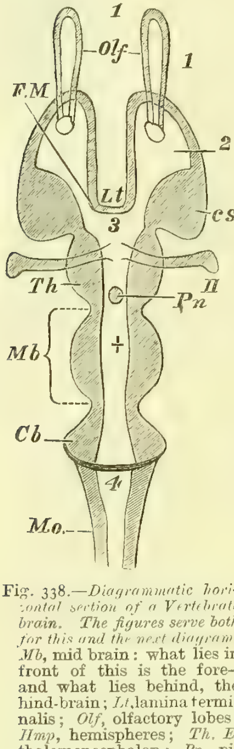


Fig. 338.—*Diagrammatic horizontal section of a Vertebrate brain. The figures serve both for this and the next diagram.* *Mb*, mid brain : what lies in front of this is the fore-, and what lies behind, the hind-brain ; *Lt*, lamina terminalis ; *Olf*, olfactory lobes ; *Hmp*, hemispheres ; *Th. E*, thalamencephalon ; *Pn*, pineal gland ; *Py*, pituitary body ; *F. M*, foramen of Munro ; *cs*, corpus striatum ; *Th*, optic thalamus ; *CC*, crura cerebri : the mass lying above the canal represents the corpora quadrigemina ; *Cb*, cerebellum ; *I—IX.*, the nine pairs of cranial nerves ; 1, olfactory ventricle ; 2, lateral ventricle ; 3, third ventricle ; 4, fourth ventricle ; +, iter a tertio ad quartum ventriculum. (Huxley.)

Chemical Composition.— The chemistry of nerve and nerve cells has been chiefly studied in the brain and spinal cord. Nerve matter contains several albuminous and fatty bodies (cerebrin, lecithin, and some others), also fatty matter which can be extracted by ether (including cholesterin) and various salts, especially Potassium and Magnesium phosphates, which exist in larger quantity than those of Sodium and Calcium. Yolk of egg resembles cerebral substance very closely in its chemical composition ; milk and muscle also come very near it.

The great relative and absolute size of the Cerebral hemispheres in the adult man, masks to a great extent the real arrangement of the several parts of the brain, which is illustrated in the two accompanying diagrams.

From these it is apparent that the parts of the brain are disposed in a linear series, as follows (from before backwards) : olfactory lobes, cerebral hemispheres, optic thalami, and third ventricle, corpora quadrigemina, or optic lobes, cerebellum, medulla oblongata.

This linear arrangement of parts actually occurs in the human fœtus (see Chapter on Development), and it is permanent in some of the lower Vertebrata, *e.g.*, Fishes, in which the cerebral hemispheres are represented by a pair of ganglia intervening between the olfactory and the optic lobes, and considerably smaller than the latter. In Amphibia the cerebral lobes are further developed, and are larger than any of the other ganglia.

In Reptiles and Birds the cerebral ganglia attain a still further development, and in Mammalia the cerebral hemispheres exceed in weight all the rest of the brain. As we ascend the scale, the relative size of the cerebrum increases, till in the higher apes and man the hemispheres, which commenced as two little lateral buds from the anterior cerebral vesicle, have grown upwards and backwards, completely covering in and hiding from view all the rest of the brain. At the same time the smooth surface of the brain, in many lower Mammalia, such as the rabbit, is replaced by the labyrinth of convolutions of the human brain.

Weight of the Brain.—The brain of an adult man weighs from 48 to 50 oz. —or about 3 lbs. It exceeds in absolute weight that of all the lower animals except the elephant and whale. Its weight, *relatively to that of the body.* is only exceeded by that of a few small birds and some of the smaller monkeys. In the adult man it ranges from $\frac{1}{30}$—$\frac{1}{50}$ of the body weight.

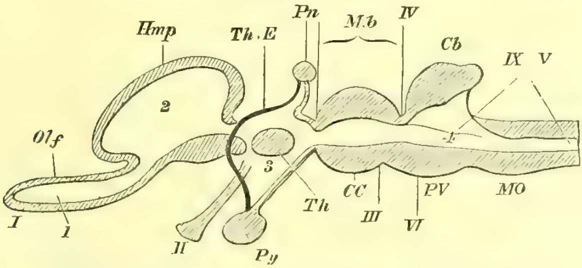


Fig. 339.—*Longitudinal and vertical Diagrammatic section of a Vertebrate brain.* Letters as before. Lamina terminalis is represented by the strong black line joining *Pn* and *Py*. (Huxley.)

Variations. Age.—In a new-born child the brain (weighing 10—14 oz.) is $\frac{1}{10}$ of the body weight. At the age of 7 years the weight of the brain already averages 40 oz.. and about 14 years the brain not unfrequently reaches the weight of 48 oz. Beyond the age of 40 years the weight slowly but steadily declines at the rate of about 1 oz. in 10 years.

Sex.—The average weight of the female brain is less than the male ; and this difference persists from birth throughout life. In the adult it amounts to about 5 oz. Thus the average weight of an adult woman's brain is about 44 oz.

Intelligence.—The brains of idiots are generally much below the average. some weighing less than 16 oz. Still the facts at present collected do not warrant more than a very general statement, to which there are numerous exceptions, that the brain weight corresponds to some extent with the degree of intelligence. There can be little doubt that the *complexity* and *depth* of the convolutions, which indicate the area of the grey matter of the cortex, correspond with the degree of intelligence (R. Wagner).

Weight of the Spinal Cord.—The *spinal cord* of man weighs from 1—1½ oz. ; its weight relatively to the brain is about 1 : 36. As we descend the scale, this ratio constantly increases till in the mouse it is 1 : 4. In cold-blooded animals the relation is reversed, the spinal cord is the heavier and the more important organ. In the newt, 2 : 1 : and in the lamprey. 75 : 1.

Distinctive Characters of the Human Brain.—The following character distinguish *the brain of man and apes from those of all other animals.* (*a*). The rudimentary condition of the olfactory lobes. (*b*). A perfectly defined fissure of Sylvius. (*c*). A posterior lobe completely covering the cerebellum. (*d*). The presence of posterior cornua in the lateral ventricles (Gratiolet).

The most *distinctive points in the human brain*, as contrasted with that of apes, are:—(1). The much greater size and weight of the whole brain. The brain of a full-grown gorilla weighs only about 15 oz., which is less than $\frac{1}{3}$ the weight of the human adult male brain, and barely exceeds that of the human infant at birth. (2). The much greater complexity of the convolutions, especially the existence in the human brain of tertiary convolutions in the sides of the fissures. (3). The greater relative size and complexity, and the blunted quadrangular contour of the frontal lobes in man, which are relatively both broader, longer, and higher, than in apes. In apes the frontal lobes project keel-like (rostrum) between the olfactory bulbs. (4). The much greater prominence of the temporo-sphenoidal lobe in apes. (5). The fissure of Sylvius is nearly horizontal in man, while in apes it slants considerably upwards. (6). The distinctness of the external perpendicular fissure, which in apes is a well-defined almost vertical "slash," while in man it is almost obscured by the annectent gyri (Rolleston).

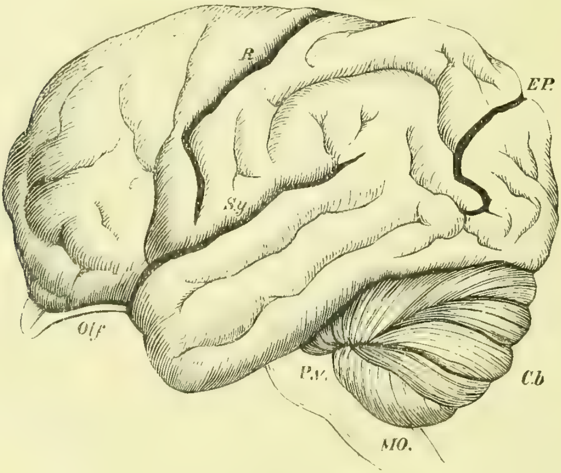


Fig. 340.—*Brain of the Orang*, $\frac{2}{3}$ natural size, showing the arrangement of the convolutions. *Sy*, fissure of Sylvius; *R*, fissure of Rolando; *EP*, external perpendicular fissure; *Olf*, olfactory lobe; *Cb*, cerebellum; *PV*, pons Varolii; *MO*, medulla oblongata. As contrasted with the human brain, the frontal lobe is short and small relatively, the fissure of Sylvius is oblique, the temporo-sphenoidal lobe very prominent, and the external perpendicular fissure very well marked. (Gratiolet.)

Most of the above points are shown in the accompanying figure of the brain of the Orang.

Functions.—(1.) The Cerebral hemispheres are the organs by which are perceived those clear and more impressive sensations which can be retained, and regarding which we can judge. (2.)

The Cerebrum is the organ of the will, in so far at least as each act of the will requires a deliberate, however quick determination. (3.) It is the means of retaining impressions of sensible things, and reproducing them in subjective sensations and ideas. (4.) It is the medium of all the higher emotions and feelings, and of the faculties of judgment, understanding, memory, reflection, induction, imagination and the like.

Evidence regarding the physiology of the cerebral hemispheres has been obtained, as in the case of other parts of the nervous system, from the study of Comparative Anatomy, from Pathology, and from Experiments on the lower animals. The chief evidences regarding the functions of the Cerebral hemispheres derived from these various sources, are briefly these :—1. Any severe injury of them, such as a general concussion, or sudden pressure by apoplexy, may instantly deprive a man of all power of manifesting externally any mental faculty. 2. In the same general proportion as the higher mental faculties are developed in the Vertebrate animals, and in man at different ages and in different individuals, the more is the size of the cerebral hemispheres developed in comparison with the rest of the cerebro-spinal system. 3. No other part of the nervous system bears a corresponding proportion to the development of the mental faculties. 4. Congenital and other morbid defects of the cerebral hemisphere are, in general, accompanied by corresponding deficiency in the range or power of the intellectual faculties and the higher instincts. 5. Removal of the cerebral hemispheres in one of the lower animals produces effects corresponding with what might be anticipated from the foregoing facts. The animal, although retaining mere sensation, and the power of performing even complicated reflex acts, remains in a state of stupor, and performs no voluntary movement of any kind. (See below.)

Effects of the Removal of the Cerebrum.—The removal of the cerebrum in the lower animals appears to reduce them to the condition of a mechanism without spontaneity. A pigeon from which the cerebrum has been removed will remain motionless and apparently unconscious unless disturbed. When disturbed in any way it soon recovers its former position; when hrown into the air it flies.

In the case of the frog, when the cerebral lobes have been removed, the animal appears similarly deprived of all power of spontaneous movement. But it sits up in a natural attitude, breathing quietly; when pricked it jumps away; when thrown into the water it swims; when placed upon the palm of the hand it remains motionless, although, if the hand be gradually tilted over till the frog is on the point of losing his balance, he will crawl up till he regains his equilibrium, and comes to be perched quite on the edge of the hand. This condition contrasts with that resulting from the removal of the entire brain, leaving only the spinal cord; in this case only the simpler reflex actions can take place. The frog does not breathe, he lies flat on the table instead of sitting up; when thrown into a vessel of water he sinks to the bottom; when his legs are pinched he kicks out, but does not leap away.

Unilateral action.—Respecting the mode in which the brain discharges its functions, there is no evidence whatever. But it appears that, for all but its highest intellectual acts, one of the cerebral hemispheres is sufficient. For numerous cases are recorded in which no mental defect was observed, although one cerebral hemisphere was so disorganised or atrophied that it could not be supposed capable of discharging its functions. The remaining hemisphere was, in these cases, adequate to the functions generally discharged by both; but the mind does not seem in any of these cases to have been tested in very high intellectual exercises; so that it is not certain that one hemisphere will suffice for these. In general, the mind combines, as one sensation, the impressions which it derives from one object through both hemispheres, and the ideas to which the two such impressions give rise are single. In relation to common sensation and the effort of the will, the impressions to and from the hemispheres of the brain are carried across the middle line; so that in destruction or compression of either hemisphere, whatever effects are produced in loss of sensation or voluntary motion, are observed on the side of he body opposite to that on which the brain is injured.

Localisation of functions.—In speaking of the cerebral hemispheres as the so-called organs of the mind, they have been regarded as if they were single organs, of which all parts are equally appropriate for the exercise of each of the mental faculties. But it is possible that each faculty has a special portion of the brain appropriated to it as its proper organ. For this theory the principal evidences are as follows :—1. That it is in accordance with the physiology of the compound organs or systems in the body, in which each part has its special function ; as, for example, of the digestive system, in which the stomach, liver, and other organs perform each their separate share in the general process of the digestion of the food. 2. That in different individuals the several mental functions are manifested in very different degrees. Even in early childhood, before education can be imagined to have exercised any influence on the mind, children exhibit various dispositions—each presents some predominant propensity, or evinces a singular aptness in some study or pursuit ; and it is a matter of daily observation that every one has his peculiar talent or propensity. But it is difficult to imagine how this could be the case, if the manifestation of each faculty depended on the whole of the brain ; different conditions of the whole mass might affect the mind generally, depressing or exalting all its functions in an equal degree, but could not permit one faculty to be strongly and another weakly manifested. 3. The plurality of organs in the brain is supported by the phenomena of some forms of mental derangement. It is not usual for all the mental faculties in an insane person to be equally disordered ; it often happens that the strength of some is increased, while that of others is diminished ; and in many cases one function only of the brain is deranged, while all the rest are performed in a natural manner. 4. The same opinion is supported by the fact that the several mental faculties are developed to their greatest strength at different periods of life, some being exercised with great energy in childhood, others only in adult age ; and that, as their energy decreases in old age, there is not a gradual and equal diminution of power in all of them at once, but, on the contrary, a diminution in one or more, while others retain their full strength, or even increase in power. 5. The plurality of cerebral organs appears to be indicated by the phenomena of dreams, in which only a part of the mental faculties are at rest or asleep, while the others are awake, and, it is presumed, are exercised through the medium of the parts of the brain appropriated to them.

Unconscious Cerebration.—In connection with the above, some remarkable phenomena should be mentioned which hav been described as depending on an *unconscious* action of the brain.

It must be within the experience of every one to have tried to recollect some particular name or occurrence: and after trying in vain for some time the attempt is given up and quite forgotten amid other occupations, when suddenly, hours or even a day or two afterwards, the desired name or occurrence unexpectedly flashes across the mind. Such occurrences are supposed by many to be due to the requisite cerebral processes going on unconsciously, and, when the result is reached, to our all at once becoming conscious of it.

That *unconscious cerebration* may sometimes occur, is likely enough; and it is paralleled by the unconscious walking of a somnambulist. But many cases of so-called unconscious cerebration are better explained by the supposition that some missing link in the chain of reasoning cannot at the moment be found; but is afterwards, by some chance combination of events, suggested, and thus the mental process is at once, with the memory of what has gone before, completed.

Again, in the vain endeavour to solve a difficult or it may be an easy problem, the reasoner is frequently in the condition of a man whose wearied muscles could never, before they have rested, overcome some obstacles. In both cases,—of brain and muscle, after renewal of their textures by rest, the task is performed so rapidly as to seem instantaneous.

Aphasia.—From the apparently greater frequency of interference with the faculty of speech in disease of the *left* than of the *right* half of the cerebrum, it has been thought that the nerve-centre for *language*, including in this term all articulate expression of ideas, is situated in the *left* cerebral hemisphere. A large number of cases are on record in which *aphasia*, or the loss of power of expressing ideas in words, has been associated with disease of the posterior part of the lower or third frontal convolution on the left side. This condition is usually associated with paralysis of the right side (right hemiplegia). The only conclusion, however, which can be drawn from this, is, that the integrity of this particular convolution is essential to the faculty of speech; we cannot conclude that it is necessarily the *centre* for language. It may be only one link in the complete chain of nervous connections necessary for the translation of an idea into articulate expression.

It seems highly probable that the corresponding right convolutions can take on the same functions as the left; and it is in this way that we can explain those cases in which recovery of speech takes place, though the *left* frontal convolution still remains diseased.

Pineal and Pituitary Bodies.

Nothing is known of the function of the pineal and pituitary bodies. They have been, indeed, supposed by some to be rather ductless glands than nervous organs (p. 472).

Experimental localisations.—Attempts have been made to localise cerebral functions by means of experiments on the lower animals. It had long been well known that the cerebral hemispheres could not be excited by mechanical, chemical, or thermal stimuli, but Fritsch and Hitzig were the first to show that they are amenable to electric irritation. They employed a weak constant current in their experiments, applying a pair of fine electrodes not more than $\frac{1}{12}$ in. apart to different parts of the cerebral cortex. The results thus obtained have been confirmed and extended by Ferrier.

The following are the fundamental phenomena observed in all these cases:

(1.) Excitation of the same spot is always followed by the same movement in the same animal. (2.) The area of excitability for any given movement is extremely small, and admits of very accurate definition. (3.) In different animals excitations of anatomically corresponding spots produce similar or corresponding results (Burdon-Sanderson).

The various definite movements resulting from the electric stimulation of circumscribed areas of the cerebral cortex, are enumerated in the description of the accompanying figures of the dog and monkey's brain.

In the case of the dog, the results obtained are summed up as follows, by Hitzig.

(*a.*) One portion (anterior) of the convexity of the cerebrum is motor; another portion (posterior) is non motor. (*b.*) Electric stimulation of the motor portion produces co-ordinated muscular contraction on the opposite side of the body. (*c.*) With very weak currents, the contractions produced are distinctly limited to particular groups of muscles; with stronger currents the stimulus is communicated to other muscles of the same or neighbouring parts. (*d.*) The portions of the brain intervening between these motor centres are inexcitable by similar means.

With regard to the facts above mentioned, all experimenters are agreed, but there is still considerable diversity of opinion as to their explanation.

It is evident that the spots marked out on the cortex are not strictly speaking motor *centres*, for they can be removed entirely without destroying the power of voluntary motion.

Burdon - Sanderson has shown that electric stimu-

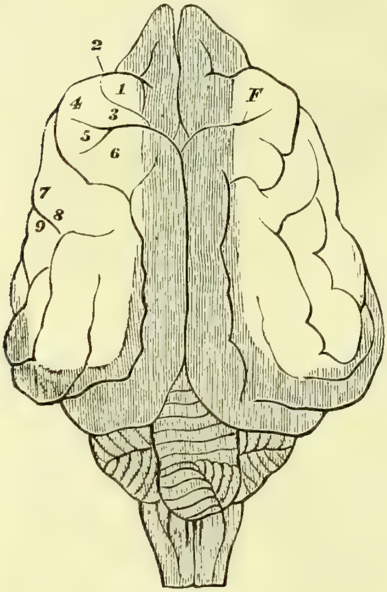


Fig. 341.

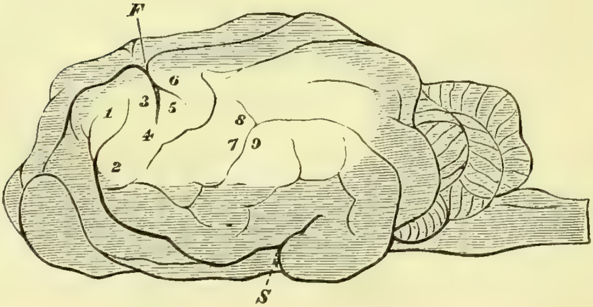


Fig. 342.

Figs. 341 and 342.—*Brain of dog, viewed from above and in profile.* *F*, frontal fissure, sometimes termed crucial sulcus, corresponding to the fissure of Rolando in man; *S*, fissure of Sylvius, around which the four longitudinal convolutions are concentrically arranged; 1, flexion of head on the neck, in the median line; 2, flexion of head on the neck, with rotation towards the side of the stimulus; 3, 4, flexion and extension of anterior limb; 5, 6, flexion and extension of posterior limb; 7, 8, 9, contraction of orbicularis oculi, and the facial muscles in general. The unshaded part is that exposed by opening the skull. (Dalton.)

lation of different points in a horizontal section, through the deeper parts of the hemispheres, produces the same effects as stimulation of the so-called "centres" in the grey matter overlying them: while the same results follow electric stimulation of different points of the corpus striatum.

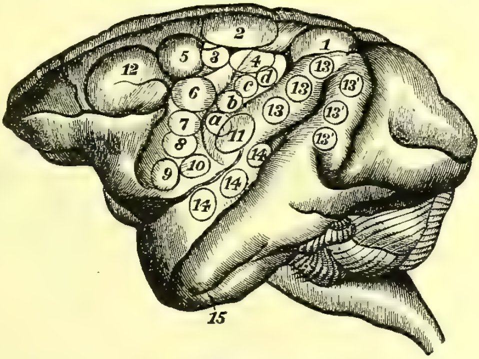


Fig. 343.

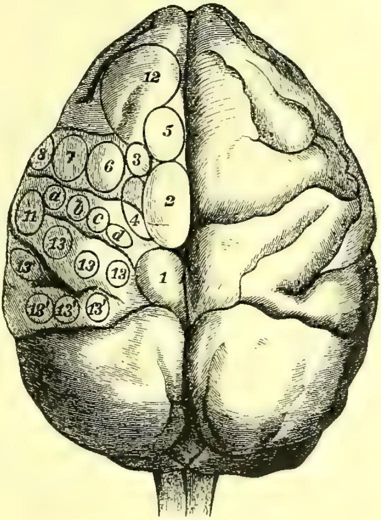


Fig. 344.

Figs. 343 and 344.—*Diagrams of monkey's brain to show the effects of electric stimulation of certain spots.* 1, movement of hind foot; 2, chiefly adduction of foot; 3, movements of hind foot and tail; 4, of latissimus dorsi; 5, extension forward of arm; *a*, *b*, *c*, *d*, movements of hand and wrist; 6, supination and flexion of forearm; 7, elevation of upper lip; 8, conjoint action of elevation of upper lip and depression of lower; 9, opening of mouth and protrusion of tongue; 10, retraction of tongue; 11, action of platysma; 12, elevation of eyebrows and eyelids, dilatation of pupils, and turning head to opposite side; 13, eyes directed to opposite side and upwards, with usually contraction of the pupils; 13′, similar action, but eyes usually directed downwards; 14, retraction of opposite ear, head turns to the opposite side, the eyes widely opened and pupils dilated; 15, stimulation of this region, which corresponds to the tip of the uncinate convolution, causes torsion of the lip and nostril of the same side. (Ferrier.)

In applying the facts ascertained by these experiments to elucidate the physiology of the human brain, we must remember that the method of electric stimulation is an artificial one, differing widely from the ordinary stimuli to which the brain is subject during life.

Functions of Other parts of the Brain.—Of the physiology of the other parts of the brain, little or nothing can be said.

Of the offices of the *corpus callosum*, or great transverse and oblique commissure of the brain, nothing positive is known. But instances in which it was absent, or very deficient, either without any evident mental defect, or with only such as might be ascribed to coincident affections of other parts, make it probable that the office which is commonly assigned to it, of enabling the two sides of the brain to act in concord, is exercised only in the highest acts of which the mind is capable. And this view is confirmed by the very late period of its development, and by its very rudimentary condition (Flower) in all but the placental Mammalia.

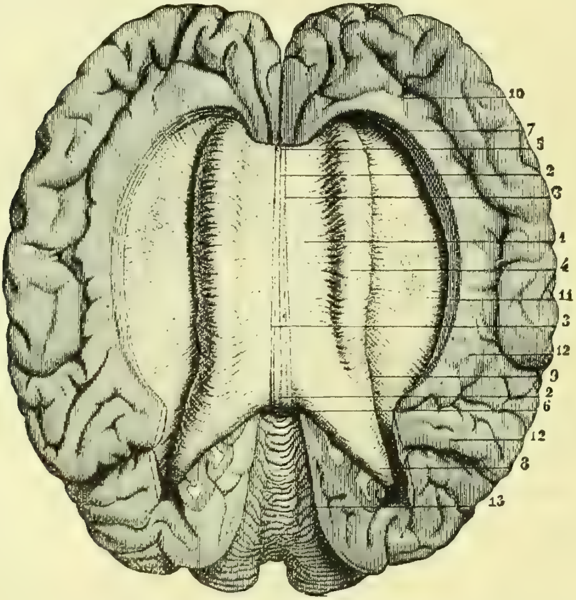


Fig. 345.—*View of the corpus callosum from above.* ½.—The upper surface of the corpus callosum has been fully exposed by separating the cerebral hemispheres and throwing them to the side; the gyrus fornicatus has been detached, and the transverse fibres of the corpus callosum traced for some distance into the cerebral medullary substance. 1, the upper surface of the corpus callosum; 2, median furrow or raphe; 3, longitudinal striæ bounding the furrow; 4, swelling formed by the transverse bands as they pass into the cerebrum; 5, anterior extremity or knee of the corpus callosum; 6, posterior extremity; 7, anterior, and 8, posterior part of the mass of fibres proceeding from the corpus callosum; 9, margin of the swelling; 10, anterior part of the convolution of the corpus callosum; 11, hem or band of union of this convolution; 12, internal convolutions of the parietal lobe; 13, upper surface of the cerebellum. (Sappey after Foville.)

To the fornix and other commissures no special function can be assigned; but it is a reasonable hypothesis that they connect the action of the parts between which they are severally placed.

Sleep.

All parts of the body which are the seat of active change require periods of rest. The alternation of work and rest is a necessary condition of their maintenance and of the healthy performance of their functions. These alternating periods, however, differ much in duration in different cases; but, for any individual instance, they preserve a general and rather close uniformity. Thus, as before mentioned, the periods of rest and work, in the case of the heart, occupy, each of them, about half a second; in the case of the ordinary respiratory muscles the periods are about four or five times as long. In many cases, again (as of the voluntary muscles during violent exercise) while the periods during active exertion alternate very frequently, yet the expenditure goes far ahead of the repair, and, to compensate for this, an after repose of some hours becomes necessary; the rhythm being less perfect as to *time*, than in the case of the muscles concerned in circulation and respiration.

Obviously, it would be impossible that, in the case of the Brain, there should be short periods of activity and repose, or in other words, of consciousness and unconsciousness. The repose must occur at long intervals; and it must therefore be proportionately long. Hence the necessity for that condition which we call *Sleep;* a condition which seeming at first sight exceptional, is only an unusually perfect example of what occurs, at varying intervals, in every actively working portion of our bodies.

A temporary abrogation of the functions of the cerebrum imitating sleep, may occur, in the case of injury or disease, as the consequence of two apparently widely different conditions. Insensibility is equally produced by a *deficient* and an *excessive* quantity of blood within the cranium, (coma); but it was once supposed that the latter offered the truest analogy to the normal condition of the brain in sleep, and in the absence of any proof to the contrary, the brain was said to be during sleep *congested.* Direct experimental enquiry has led, however, to the opposite conclusion.

By exposing, at a circumscribed spot, the surface of the brain of living animals, and protecting the exposed part by a watch-glass, Durham was able to prove that the brain becomes visibly paler (anæmic) during sleep; and the anæmia of the optic disc during sleep, observed by Hughlings Jackson, may be taken as a strong confirmation, by analogy, of the same fact.

A very little consideration will show that these experimental results correspond exactly with what might have been foretold from the analogy of other physiological conditions. Blood is supplied to the brain for two partly distinct purposes. (1.) It is supplied for mere nutrition's sake. (2.) It is necessary for bringing supplies of potential or active energy, (*i.e.*, *combustible matter* or *heat*) which may be transformed by the cerebral corpuscles into the various manifestations of nerve-force. During sleep, blood is requisite for only the first of these purposes; and its supply in greater quantity would be not only useless, but, by supplying an excitement to work, when rest is needed, would be positively harmful. In this respect the varying circulation of blood in the brain exactly resembles that which occurs in all other energy transforming parts of the body; *e.g.*, *glands* or *muscles.*

At the same time, it is necessary to remember that the normal anæmia of the brain which accompanies sleep is probably a result and not a cause of the quiescence of the cerebral functions. What the immediate cause of this periodical partial abrogation of function is, however, we do not know.

Somnambulism and Dreams.—What we term *sleep* occurs often in very different degrees in different parts of the nervous system; and in some parts the expression cannot be used in the ordinary sense.

The phenomena of *dreams* and *somnambulism* are examples of differing degrees of sleep in different parts of the cerebro-spinal nervous system. In the former case the cerebrum is still partially active; but the mind-products of its action are no longer corrected by the reception, on the part of the sleeping *sensorium*, of impressions of objects belonging to the outer world; neither can the cerebrum, in this half-awake condition, act on the centres of reflex action of the voluntary muscles, so as to cause the latter to contract—a fact within the painful experience of all who have suffered from nightmare.

In somnambulism the cerebrum is capable of exciting that train of reflex nervous action which is necessary for progression, while the nerve-centre of *muscular sense* (in the cerebellum?) is, presumably, fully awake; but the *sensorium* is still asleep, and impressions made on it are not sufficiently *felt* to rouse the cerebrum to a comparison of the difference between mere ideas or memories and sensations derived from external objects.

Physiology of the Cranial Nerves.

The *cranial* nerves are commonly enumerated as nine pairs; but the number is in reality twelve, the seventh nerve consisting as it does, of two nerves, and the eighth of three. All arise (superficial origin) from the base of the encephalon, in a double series which extends from the under surface of the anterior cerebral lobes to the lower end of the medulla oblongata. Traced into the substance of the brain and medulla, the roots of the nerves are found connected with various masses of grey matter, which are all connected one with another, and with the cerebral hemispheres.

The roots of the olfactory *tracts* are connected deeply with the cortex of the anterior cerebral hemisphere, and probably with the corpora striata also. The optic nerves can be traced into the optic thalami, corpora quadrigemina, and corpora geniculata. The third and fourth nerves arise from grey matter beneath the corpora quadrigemina; and the roots of origin of the remainder of the cranial nerves can be traced to grey matter in the medulla oblongata beneath the floor of the fourth ventricle, and in the more central part of the medulla, around its central canal, as low down as the decussation of the pyramids.

According to their several functions, the cranial nerves may be thus arranged :—

Nerves of special sense .	Olfactory, optic, auditory, part of the glossopharyngeal, and of the lingual branch of the fifth.
,, of common sensation .	The greater portion of the fifth.
,, of motion	Third, fourth, lesser division of the fifth, sixth, facial, and hypoglossal.
Mixed nerves	Glossopharyngeal, vagus, and spinal accessory.

The physiology of the several nerves of the special senses will be considered with the organs of those senses.

Third Nerve.

Functions.—The third nerve, or *motor oculi*, supplies the levator palpebræ superioris muscle, and, of the muscles of the eye-ball, all but the superior oblique or trochlearis, to which the fourth nerve is appropriated, and the rectus externus which receives the sixth nerve. Through the medium of the ophthalmic or lenticular ganglion, of which it forms what is called the short root, it also supplies motor filaments to the iris and ciliary muscle.

When the third nerve is irritated within the skull, all those muscles to which it is distributed are convulsed. When it is *paralysed* or *divided* the following effects ensue: (1), the upper eyelid can be no longer raised by the elevator palpebræ, but droops (ptosis) and remains gently closed over the eye, under the unbalanced influence of the orbicularis palpebrarum, which is supplied by the facial nerve: (2), the eye is turned outwards (external strabismus) by the unbalanced action of the rectus externus, to which the sixth nerve is appropriated: and hence, from the irregularity of the axes of the eyes, double-sight is often experienced when a single object is within view of both the eyes: (3), the eye cannot be moved either upwards, downwards, or inwards: (4), the pupil becomes dilated (mydriasis), and insensible to light: (5), the eye cannot "accommodate" itself for vision at short distances.

Contraction and Dilatation of the Pupil.—The relation of the third nerve to the iris is of peculiar interest. In ordinary circumstances the contraction of the iris is a reflex action, which may be explained as produced by the stimulus of light on the retina being conveyed by the optic nerve to the brain (probably to the corpora quadrigemina), and thence reflected through the third nerve to the iris. Hence the iris ceases to act when either the optic or the third nerve is divided or destroyed, or when the corpora quadrigemina are destroyed or much compressed. But when the optic nerve is divided, the contraction of the iris may be excited by irritating that portion of the nerve which is connected with the brain; and when the third nerve is divided, the irritation of its distal portion will still excite the contraction of the iris.

The contraction of the iris thus shows all the characters of a reflex act, and in ordinary cases requires the concurrent action of the optic nerve, corpora quadrigemina, and third nerve; and, probably also, considering the peculiarities of its perfect mode of action, of the ophthalmic ganglion. But, besides, both irides will contract their pupils under the reflected stimulus of light falling only on one retina or under irritation of one optic nerve. Thus, in blindness of one eye, its pupil may contract when the other eye is exposed to a stronger light: and generally the contraction of each of the pupils appears to be in direct proportion to the total quantity of light which stimulates either one or both retinæ, according as one or both eyes are open.

The iris acts also in association with certain other muscles supplied by the third nerve: thus, when the eye is directed inwards, or upwards and inwards, by the action of the third nerve distributed in the rectus internus and rectus superior, the iris contracts, as if under direct voluntary influence. The will cannot, however, act on the iris alone through the third nerve; but this aptness to contract in association with the other muscles supplied by the third, may be sufficient to make it act even in total blindness and insensibility of the retina, whenever these muscles are contracted. The contraction of the pupils, when the eyes are moved inwards, as in looking at a near object, has probably the purpose of excluding those outermost rays of light which would be too far divergent to be refracted to a clear image on the retina; and the dilatation in looking straight forwards as in looking at a distant object, permits the admission of the largest number of rays, of which none are too divergent to be so refracted. (For further remarks on the contraction and dilatation of the pupil, see p. 702.)

Fourth Nerve.

Functions.—The fourth nerve, or *Nervus trochlearis* or *patheticus,* is exclusively motor, and supplies only the trochlearis or obliquus superior muscle of the eyeball.

Fifth or Trigeminal Nerve.

Functions.—The fifth or trigeminal nerve resembles, as already stated, the spinal nerves, in that its branches are derived through two roots; namely, the larger or *sensory*, in connection with which is the Gasserian ganglion, and the smaller or *motor* root which has no ganglion, and which passes under the ganglion of the sensory root to join the third branch or division which issues from it. The first and second divisions of the nerve, which arise wholly from the larger root, are purely sensory. The third division being joined, as before said, by the motor root of the nerve, is of course both motor and sensory.

(a.) **Motor Functions.**—Through branches of the lesser or non-ganglionic portion of the fifth, the muscles of mastication, namely, the temporal, masseter, two pterygoid, anterior part of the digastric, and mylo-hyoid, derive their motor nerves. Filaments are also supplied to the tensor tympani and tensor palati. The motor function of these branches is proved by the violent contraction of all the muscles of mastication in experimental irritation of the third or inferior maxillary division of the nerve; by paralysis of the same muscles, when it is divided or disorganised, or from any reason deprived of power; and by the retention of the power of these muscles, when all those supplied by the facial nerve lose their power through paralysis of that nerve. The last instance proves best, that though the buccinator muscle gives passage to, and receives some filaments from, a buccal branch of the inferior division of the fifth nerve, yet it derives its motor power from the facial, for it is paralysed together with the other muscles that are supplied by the facial, but retains its power when the other muscles of mastication are paralysed. Whether, however, the branch of the fifth nerve which is supplied to the buccinator muscle is entirely sensory, or in part motor also, must remain for the present doubtful. From the fact that this muscle, besides its other functions, acts in concert or harmony with the muscles of mastication, in keeping the food between the teeth, it might be supposed from analogy, that it would have a motor branch from the same nerve that supplies them. There can be no doubt, however, that the so-called buccal branch of the fifth is, in the main, sensory; although it is not quite certain that it does not give a few motor filaments to the buccinator muscle.

(b.) **Sensory Functions.**—Through the branches of the greater or ganglionic portion of the fifth nerve, all the anterior and antero-lateral parts of the face and head, with the exception of the skin of the parotid region (which derives branches from the cervical spinal nerves), acquire common sensibility; and among these parts may be included the organs of special sense, from which common sensations are conveyed through the fifth nerve, and their special sensations through their several nerves of special sense. The muscles, also, of the face and lower jaw acquire muscular sensibility, through the filaments of the ganglionic portion of the fifth nerve distributed to them with their proper motor nerves. The sensory function of the branches of the greater division of the fifth nerve is proved, by all the usual evidences, such as their distribution in parts that are sensitive and not capable of muscular

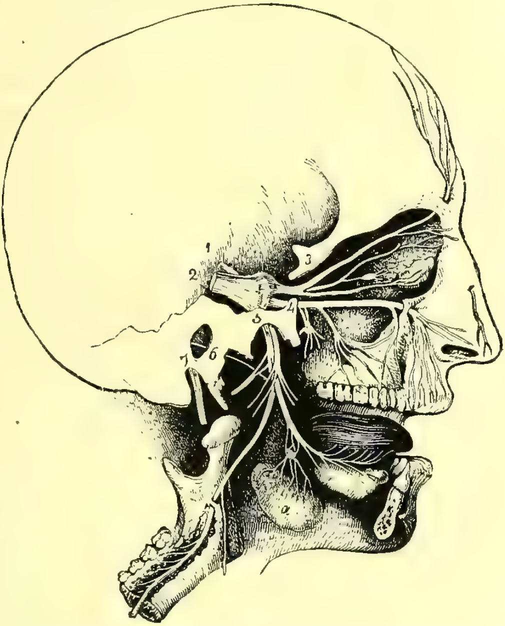


Fig. 346.—*General plan of the branches of the fifth pair.* ⅓.—1, lesser root of the fifth pair; 2, greater root passing forwards into the Gasserian ganglion; 3, placed on the bone above the ophthalmic nerve, which is seen dividing into the supra-orbital, lachrymal, and nasal braches, the latter connected with the ophthalmic ganglion; 4, placed on the bone close to the foramen rotundum, marks the superior maxillary division, which is connected below with the spheno-palatine ganglion, and passes forwards to the infraorbital foramen; 3, placed on the bone over the foramen ovale, marks the inferior maxillary nerve, giving off the anterior auricular and muscular branches, and continued by the inferior dental to the lower jaw, and by the gustatory to the tongue; *a*, the submaxillary gland, the submaxillary ganglion placed above it in connection with the gustatory nerve; 6, the chorda tympani; 7, the facial nerve issuing from the stylomastoid foramen. (Charles Bell.)

contraction, the exceeding sensibility of some of these parts, their loss of sensation when the nerve is paralysed or divided, the pain without convulsions produced by morbid or experimental irritation of the trunk or branches of the nerve, and the analogy of this portion of the fifth to the posterior root of the spinal nerve.

Other Functions.—In relation to *muscular movements*, the branches of the greater or ganglionic portion of the fifth nerve exercise a manifold influence on the movements of the muscles of the head and face, and other parts in which they are distributed. They do so, in the first place (*a*), by providing the muscles themselves with that sensibility without which the mind, being unconscious of their position and state, cannot voluntarily exercise them. It is, probably, for conferring this sensibility on the muscles, that the branches of the fifth nerve communicate so frequently with those of the facial and hypoglossal, and the nerves of the muscles of the eye; and it is because of the loss of this sensibility that when the fifth nerve is divided, animals are always slow and awkward in the movement of the muscles of the face and head, or hold them still, or guide their movements by the sight of the objects towards which they wish to move.

Again, the fifth nerve has an indirect influence on the muscular movements, by (*b*) conveying sensations of the state and position of the skin and other parts: which the mind perceiving, is enabled to determine appropriate acts. Thus, when the fifth nerve or its infra-orbital branch is divided, the movements of the lips in feeding may cease, or be imperfect. Bell supposed that the motion of the upper lip in grasping food depended directly on the infra-orbital nerve; for he found that, after he had divided that nerve on both sides in an ass, it no longer seized the food with its lips, but merely pressed them against the ground, and used the tongue for the prehension of the food. Mayo corrected this error. He found, indeed, that after the infra-orbital nerve had been divided, the animal did not seize its food with the lip, and could not use it well during mastication, but that it could open the lips. He, therefore, justly attributed the phenomena in Bell's experiments to the loss of sensation in the lips; the animal not being able to feel the food, and, therefore, although it had the power to seize it, not knowing how or where to use that power.

The fifth nerve has also (*c*), an intimate connection with muscular movements through the many reflex acts of muscles of which it is the necessary excitant. Hence, when it is divided and can no longer convey impressions to the nervous centres to be thence reflected, the irritation of the conjunctiva produces no closure of the eye, the mechanical irritation of the nose excites no sneezing.

Through its ciliary branches and the branch which forms the long root of the ciliary or ophthalmic ganglion, it exercises also (*d*), some influence on the movements of the iris.

When the trunk of the ophthalmic portion is divided, the pupil becomes, according to Valentin, contracted in men and rabbits, and dilated in cats and dogs; but in all cases, becomes immovable even under all the varieties of the stimulus of light. How the fifth nerve thus affects the iris is unexplained; the same effects are produced by destruction of the superior cervical ganglion of the sympathetic, so that, possibly, they are due to the injury of those filaments of the sympathetic which, after joining the trunk of the fifth, at and beyond the Gasserian ganglion, proceed with the branches of its ophthalmic division to the iris; or, as R. Hall ingeniously suggests, the influence of the fifth nerve on the movements of the iris may be ascribed to the affection of vision in consequence of the disturbed circulation or nutrition in the retina, when the normal influence of the fifth nerve and ciliary ganglion is disturbed. In such disturbance, increased circulation making the retina more irritable might induce extreme contraction of the iris; or under moderate stimulus of light, producing partial blindness, might induce dilatation: but it does not appear why, if this be the true explanation, the iris should in either case be immovable and unaffected by the various degrees of light.

Trophic influence. — Furthermore, the morbid effects which division of the fifth nerve produces in the organs of special sense, make it probable that, in the normal state, the fifth nerve exercises some *trophic* influence on all these organs; although, in part, the effect of the section of the nerve is only indirectly destructive by abolishing sensation, and therefore the natural safeguard which leads to the protection of parts from external injury. Thus, after such division, within a period varying from twenty-four hours to a week, the cornea begins to be opaque; then it grows completely white; a low destructive inflammatory process ensues in the conjunctiva, sclerotica, and interior parts of the eye; and within one or a few weeks, the whole eye may be quite disorganised, and the cornea may slough or be penetrated by a large ulcer. The sense of smell (and not merely that of mechanical irritation of the nose), may be at the same time lost or gravely impaired; so may the hearing, and commonly, whenever the fifth nerve is paralysed, the tongue loses the sense of taste in its anterior and lateral parts, *i.e.*, in the portion in which the lingual or gustatory branch of the inferior maxillary division of the fifth is distributed.

In relation to Taste.—The loss of the sense of taste is no doubt due (*a*) to the lingual branch of the fifth nerve being a nerve of special sense; partly, also, it is due (*b*), to the fact that this branch supplies, in the anterior and lateral parts of the tongue, a necessary condition for the proper nutrition of that part; while (*c*), it forms also one chief link in the nervous circle for reflex action, in the secretion of saliva (p. 285). But, deferring this question until the glosso-pharyngeal nerve is to be considered, it may be observed that in some brief time after complete paralysis or division of the fifth nerve, the power of all the organs of the special senses may be lost; they may lose not merely their sensibility to common impressions, for which they all depend directly on the fifth nerve, but also their sensibility to their several peculiar impressions for the reception and conduction of which they are purposely constructed and supplied with special nerves besides the fifth. The facts observed in these cases can, perhaps, be only explained by the influence which the fifth nerve exercises on the nutritive processes in the organs of the special senses. It is not unreasonable to believe, that, in paralysis of the fifth nerve, their tissues may be the seats of such changes as are seen in the laxity, the vascular congestion, œdema, and other affections of the skin of the face and other tegumentary parts which also accompany the paralysis; and that these changes, which may appear unimportant when they affect external parts, are sufficient to destroy that refinement of structure by which the organs of the special senses are adapted to their functions.

That complete paralysis of the fifth nerve may be unaccompanied, at least.

for a considerable period, by injury to the organs of special sense, with the exception of that portion of the tongue which is supplied by its gustatory branch, is well illustrated by a valuable case recorded by Althaus.

According to Magendie and Longet, destruction of the eye ensues more quickly after division of the trunk of the fifth beyond the Gasserian ganglion, or after division of the ophthalmic branch, than after division of the roots of the fifth between the brain and the ganglion. Hence it would appear as if the influence on nutrition were conveyed in part through the filaments of the sympathetic, which join the branches of the fifth nerve at and beyond the Gasserian ganglion.

The existence of ganglia of the sympathetic in connection with all the principal divisions of the fifth nerve where it gives off those branches which supply the organs of special sense—for example, the connection of the ophthalmic ganglion with the ophthalmic nerve at the origin of the ciliary nerves; of the spheno-palatine ganglion with the superior maxillary division, where it gives its branches to the nose and the palate; of the otic ganglion with the inferior maxillary near the giving off of filaments to the internal ear; and of the sub-maxillary ganglion with the lingual branch of the fifth —all these connections suggest that a peculiar and probably conjoint influence of the sympathetic and fifth nerves is exercised in the nutrition of the organs of the special senses; and the results of experiment and disease confirm this, by showing that the nutrition of the organs may be impaired in consequence of impairment of the power of either of the nerves.

In relation to Sight.—A possible but doubtful connection between the fifth nerve and the sense of sight, has been thought to be shown in cases in which blows or other injuries implicating the frontal nerve as it passes over the brow, are followed by total blindness in the corresponding eye. In some cases the blindness occurs at once, probably from concussion of the retina; but in others it is very slowly progressive, as if from defective nutrition of the retina and may be accompanied with inflammatory disorganisation, like that previously referred to (p. 625). The connection of the fifth nerve with the result must, however, be considered very doubtful.

Sixth Nerve.

Functions.—The sixth nerve, *Nervus abducens* or *ocularis externus*, is also, like the fourth, exclusively motor, and supplies only the rectus externus muscle.

The rectus externus is convulsed, and the eye is turned outwards, when the sixth nerve is irritated; and the muscle is paralysed when the nerve is divided. In all such cases of paralysis, the eye squints inwards, and cannot be moved outwards.

In its course through the cavernous sinus, the sixth nerve forms larger communications with the sympathetic nerve than any other nerve within the cavity of the skull does. But the import of these communications with the sympathetic, and the subsequent distribution of its filaments after joining the sixth nerve, are quite unknown.

Seventh or Facial Nerve.

Functions.—The facial, or *portio dura* of the seventh pair of nerves, is the motor nerve of all the muscles of the face, including the platysma, but not including any of the muscles of mastication already enumerated (p. 278); it supplies, also, the parotid gland, and through the connection of its trunk with the Vidian nerve, by the petrosal nerves, some of the muscles of the soft palate, probably the levator palati and azygos uvulæ; by its tympanic branches it supplies the stapedius and laxator tympani, and, through the otic ganglion, the tensor tympani; through the *chorda tympani* it sends branches to the submaxillary gland and to the lingualis and some other muscular fibres of the tongue; and by branches given off before it comes upon the face, it supplies the muscles of the external ear, the posterior part of the digastricus, and the stylohyoideus.

Besides its *motor* influence, the facial is also, by means of the fibres which are supplied to the submaxillary and parotid glands, a *secretory* nerve. For, through the last-named branches, impressions may be conveyed which excite increased secretion of saliva (p. 286).

Symptoms of Paralysis of Facial Nerve.—When the facial nerve is divided, or in any other way paralysed, the loss of power in the muscles which it supplies, while proving the nature and extent of its functions, displays also the necessity of its perfection for the perfect exercise of all the organs of the special senses. Thus, in paralysis of the facial nerve, the orbicularis palpebrarum being powerless, the eye remains open through the unbalanced action of the levator palpebræ; and the conjunctiva, thus continually exposed to the air and the contact of dust, is liable to repeated inflammation, which may end in thickening and opacity of both its own tissue and that of the cornea. These changes, however, ensue much more slowly than those which follow paralysis of the fifth nerve, and never bear the same destructive character.

The sense of hearing, also, is impaired in many cases of paralysis of the facial nerve; not only in such as are instances of simultaneous disease in the auditory nerves, but in such as may be explained by the loss of power in the muscles of the internal ear. The sense of smell is commonly at the same time impaired through the inability to draw air briskly towards the upper part of the nasal cavities in which part alone the olfactory nerve is distributed; because, to draw the air perfectly in this direction, the action of the dilators and compressors of the nostrils should be perfect.

Lastly, the sense of taste is impaired, or may be wholly lost in paralysis of the facial nerve, provided the source of the paralysis be in some part of the nerve between its origin and the giving off of the chorda tympani. This result, which has been observed in many instances of disease of the facial nerve in man, appears explicable by the influence which, through the chorda tympani, it exercises on the movements of the lingualis and the adjacent muscular fibres of the tongue; and on the process of secretion of saliva.

Together with these effects of paralysis of the facial nerve, the muscles of the face being all powerless, the countenance acquires on the paralysed side a characteristic, vacant look, from the absence of all expression: the angle of the mouth is lower, and the paralysed half of the mouth looks longer than that on the other side; the eye has an unmeaning stare. All these peculiarities increase, the longer the paralysis lasts; and their appearance is exaggerated when at any time the muscles of the opposite side of the face are made active in any expression, or in any of their ordinary functions. In an attempt to blow or whistle, one side of the mouth and cheek acts properly, but the other side is motionless, or flaps loosely at the impulse of the expired air; so in trying to suck, one side only of the mouth acts; in feeding, the lips and cheek are powerless, and food lodges between the cheek and gum.

Glosso-Pharyngeal Nerve.

The glosso-pharyngeal nerves (16, fig. 347), in the enumeration of the cerebral nerves by numbers according to the position in which they leave the cranium, are considered as divisions of the *eighth pair of nerves*, in which term are included with them the pneumogastric and accessory nerves. But the union of the nerves under one term is inconvenient, although in some parts the glosso-pharyngeal and pneumogastric are so combined in their distribution that it is impossible to separate them in either their anatomy or physiology.

Distribution.—The glosso-pharyngeal nerve gives filaments through its tympanic branch (Jacobson's nerve), to the fenestra ovalis, and fenestra rotunda, and the Eustachian tube ; also, to the carotid plexus, and, through the petrosal nerve, to the spheno-palatine ganglion. After communicating, either within or without the cranium, with the pneumogastric, and soon after it leaves the cranium, with the sympathetic, digastric branch of the facial, and the accessory nerve, the glosso-pharyngeal nerve parts into the two principal divisions indicated by its name, and supplies the mucous membrane of the posterior and lateral walls of the upper part of the pharynx, the Eustachian tube, the arches of the palate, the tonsils and their mucous membrane, and the tongue as far forwards as the foramen cæcum in the middle line, and to near the tip at the sides and inferior part.

Functions.—The glosso-pharyngeal nerve contains some motor fibres, together with those of common sensation and the sense of taste.

1. The muscles which receive filaments from the glosso-pharyngeal are the stylo-pharyngei, palato-glossi, and constrictors of the pharynx.

Besides being (2) a nerve of common sensation in the parts which it supplies, and a centripetal nerve through which impressions are conveyed to be reflected to the adjacent muscles, the glosso-pharyngeal is also a nerve of special sensation ; being the nerve of taste, in all the parts of the tongue and palate to which it is distributed. After many discussions, the question, Which is the nerve of taste?—the lingual branch of the fifth, or the glosso-pharyngeal? — may be most probably answered by stating that they are both nerves of this special function. For very numerous experiments and cases have shown that when the trunk of the fifth nerve or its lingual branch is paralysed or divided, the sense of taste is completely lost in the superior surface of the anterior and lateral parts of the tongue. The loss is instantaneous after division of the nerve; and, therefore, cannot be ascribed to the defective nutrition of the part, though to this, perhaps, may be ascribed the more complete and general loss of the sense of taste when the whole of the fifth nerve has been paralysed.

But, on the other hand, while the loss of taste in the part of the tongue to which the lingual branch of the fifth nerve is distributed proves that to be a gustatory nerve, the fact that the sense of taste is at the same time retained in the posterior and postero-lateral parts of the tongue, and in the soft palate and its anterior arch, to which (and to some parts of which exclusively) the glosso-pharyngeal is distributed, proves that this also must be a nerve of taste.

Pneumogastric or Vagus Nerve.

Distribution.—The *pneumogastric nerve*, *nervus vagus*, or *par vagum* (1, fig. 347), has, of all the cranial and spinal nerves, the most various distribution, and influences the most various functions, either through its own filaments, or those which, derived from other nerves, are mingled in its branches. The parts supplied by the branches of the vagus nerve are as follows: by its pharyngeal branches, which enter the pharyngeal plexus, a large portion of the mucous membrane, and, probably, all the muscles of the Pharynx; by the superior laryngeal nerve, the mucous membrane of the under surface of the Epiglottis, the Glottis, and the greater part of the Larynx, and, the crico-thyroid muscle; by the inferior laryngeal nerve, the mucous membrane and muscular fibres of the Trachea, the lower part of the pharynx and larynx, and all the muscles of the larynx except the crico-thyroid; by œsophageal branches, the mucous membrane and muscular coats of the Œsophagus. Moreover, the branches of the vagus form a large portion of the supply of nerves to the Heart and the great Arteries through the cardiac nerves, derived from both the trunk and the recurrent nerve; to the

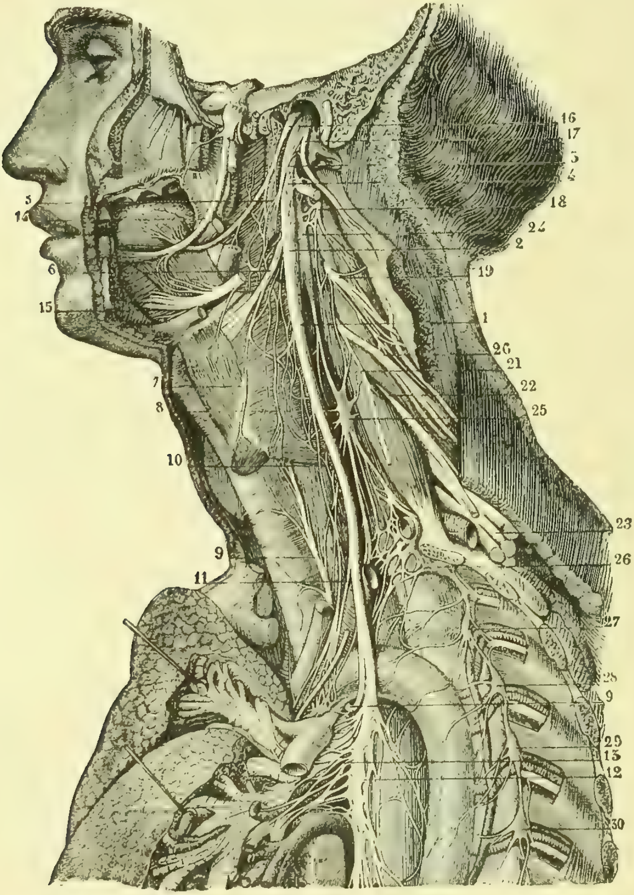


Fig. 317.—*View of the nerves of the eighth pair*, their distribution and connections on the left side. $\frac{2}{5}$.—1, pneumogastric nerve in the neck; 2, ganglion of its trunk; 3, its union with the spinal accessory; 4, its union with the hypoglossal; 5, pharyngeal branch; 6, superior laryngeal nerve; 7, external laryngeal; 8, laryngeal plexus; 9, inferior or recurrent laryngeal; 10, superior cardiac branch; 11, middle cardiac; 12, plexiform part of the nerve in the thorax; 13, posterior pulmonary plexus; 14, lingual or gustatory nerve of the inferior maxillary; 15, hypoglossal, passing into the muscles of the tongue, giving its thyroid-hyoid branch, and uniting with twigs of the lingual; 16, glosso-pharyngeal nerve; 17, spinal accessory nerve, uniting by its inner branch with the pneumogastric, and by its outer, passing into the sterno-mastoid muscle; 18, second cervical nerve; 19, third; 20, fourth; 21, origin of the phrenic nerve, 22, 23, fifth, sixth, seventh, and eighth cervical nerves, forming with the first dorsal the brachial plexus; 24, superior cervical ganglion of the sympathetic; 25, middle cervical ganglion; 26, inferior cervical ganglion united with the first dorsal ganglion; 27, 28, 29, 30, second, third, fourth, and fifth dorsal ganglia. (From Sappey after Hirschfeld and Leveillé).

Lungs, through both the anterior and the posterior pulmonary plexuses; and to the Stomach, by its terminal branches passing over the walls of that organ; while branches are also distributed to the Liver and to the Spleen.

Communications.—Throughout its whole course, the vagus contains both sensory and motor fibres; but after it has emerged from the skull, and, in some instances even sooner, it enters into so many anastomoses that it is hard to say whether the filaments it contains are, from their origin, its own, or whether they are derived from other nerves combining with it. This is particularly the case with the filaments of the sympathetic nerve, which are abundantly added to nearly all its branches. The likeness to the sympathetic which it thus acquires is further increased by its containing many filaments derived, not from the brain, but from its own petrosal ganglia, in which filaments originate, in the same manner as in the ganglia of the sympathetic, so abundantly that the trunk of the nerve is visibly larger below the ganglia than above them (Bidder and Volkmann). Next to the sympathetic nerve, that which most communicates with the vagus is the accessory nerve, whose internal branch joins its trunk, and is lost in it.

Functions.—The most probable account of the particular functions which the branches of the pneumogastric nerve discharge in the several parts to which they are distributed, may be drawn from John Reid's experiments on dogs. They show that,—1. The *pharyngeal* branch is the principal *motor* nerve of the pharynx and soft palate, and is most probably wholly motor; the chief part of its motor fibres being derived from the internal branch of the accessory nerve. 2. The *inferior* or *recurrent laryngeal* nerve is the motor nerve of the larynx. 3. The *superior laryngeal* nerve is chiefly sensory: the only muscle supplied by it being the crico-thyroid. 4. The motions of the *œsophagus*, the stomach and part of the small intestines are dependent on motor fibres of the vagus, and are probably excited by impressions made upon sensitive fibres of the same. 5. The *cardiac* branches communicate, from the centre in the medullary channel, impulses (inhibitory) regulating the action of the heart. 6. The *pulmonary* branches form the principal channel by which the sensory impressions on the mucous surface of the trachea, bronchi and lungs that influence respiration are transmitted to the medulla oblongata;

and some fibres also supply motor influence to the muscular portions of the fibres of the trachea and bronchi. 7. Branches to the stomach and intestine not only convey motor but also *vaso-motor* impulses to those organs. 8. The action of the so-called *depressor* branch (p. 192) in *inhibiting the action of the vaso-motor centre* has already been treated of, as has also the influence of the vagus in stimulating the secretion of the salivary glands, as in the nausea which precedes vomiting (p. 286). To summarise, therefore, the many functions of this nerve, it may be said that it supplies *motor* influence to the pharynx and œsophagus, to stomach and small intestine, and to the larynx, trachea, bronchi and lung; *sensory* and in part *vaso-motor* influence to the same regions; *inhibitory* influence to the heart; *inhibitory* afferent impulses to the vaso-motor centre; *excito-secretory* to the salivary glands; *excito-motor* in coughing, vomiting, &c.

Effects of Section.—Division of both vagi, or of both their recurrent branches, is often very quickly fatal in young animals; but in old animals the division of the recurrent nerve is not generally fatal, and that of both the vagi is not always fatal, and, when it is so, death ensues slowly. This difference is, probably, because, the yielding of the cartilages of the larynx in young animals permits the glottis to be closed by the atmospheric pressure in inspiration, and they are thus quickly suffocated unless tracheotomy be performed. In old animals, the rigidity and prominence of the arytenoid cartilages prevent the glottis from being completely closed by the atmospheric pressure; even when all the muscles are paralysed, a portion at its posterior part remains open, and through this the animal continues to breathe.

In the case of slower death, after division of both the vagi, the lungs are commonly found gorged with blood, œdematous, or nearly solid, with a kind of low pneumonia, and with their bronchial tubes full of frothy bloody fluid and mucus, changes to which, in general, the death may be proximately ascribed. These changes are due, perhaps in part, to the influence which the nerves exercise on the movements of the air-cells and bronchi; yet, since they are not always produced in one lung when its nerve is divided, they cannot be ascribed wholly to the suspension of organic nervous influence. Rather, they may be ascribed to the hindrance to the passage of blood through the lungs, in consequence of the diminished supply of air and the excess of carbonic acid in the air-cells and in the pulmonary capillaries; in part, perhaps, to paralysis of the blood-vessels, leading to congestion; and in part, also, they appear due to the passage of food and of the various secretions of the mouth and fauces through the glottis, which, being deprived of its sensibility, is no longer stimulated or closed in consequence of their contact.

References to other functions of Vagi.—Regarding the influence of the vagus, see also Heart (p. 156), Arteries (p. 192), Salivary Gland (p. 286), Glottis and Larynx (p. 250), Trachea and Bronchi (p. 227), Lungs (p. 250), Pharynx and Œsophagus (p. 296), Stomach (p. 312).

Spinal Accessory Nerve.

The principal branch of the accessory nerve, its external branch, supplies the sterno-mastoid and trapezius muscles; and, though pain is produced by irritating it, is composed almost exclusively of motor fibres. It is very probable that the accessory nerve gives some motor filaments to the vagus. For, among the experiments made on this point, many have shown that when the accessory nerve is irritated within the skull, convulsive movements ensue in some of the muscles of the larynx; all of which, as already stated, are supplied, apparently, by branches of the vagus; and (which is a very significant fact) Vrolik states that in the chimpanzee the internal branch of the accessory does not join the vagus at all, but goes direct to the larynx.

Among the roots of the accessory nerve, the lower, arising from the spinal cord, appear to be composed exclusively of motor fibres, and to be destined entirely to the trapezius and sterno-mastoid muscles; the upper fibres, arising from the medulla oblongata, contain many sensory as well as motor fibres.

Hypoglossal Nerve.

Distribution.—The hypoglossal or ninth nerve, or *motor linguæ*, has a peculiar relation to the muscles connected with the hyoid bone, including those of the tongue. It supplies through its descending branch (*descendens noni*), the sterno-hyoid, sterno-thyroid, and omo-hyoid; through a special branch of the thyro-hyoid, and through its lingual branches the genio-hyoid, styloglossus, hyo-glossus, and genio-hyo-glossus and linguales. It contributes, also, to the supply of the submaxillary gland.

Functions.—The function of the hypoglossal is exclusively motor, except in so far as its descending branch may receive a few sensory filaments from the first cervical nerve. As a motor nerve, its influence on all the muscles enumerated above is shown by their convulsions when it is irritated, and by their loss of power when it is paralysed. The effects of the paralysis of one hypoglossal nerve are, however, not very striking in the tongue. Often, in cases of hemiplegia involving the functions of the hypoglossal nerve, it is not possible to observe any deviation in the direction of the protruded tongue; probably because the tongue is so compact and firm that the muscles on either side, their insertion being nearly parallel to the median line, can push it straight forwards or turn it for some distance towards either side.

Spinal Nerves.

Functions.—Little need be added to what has been already said of these nerves (pp. 569 to 573). The anterior roots of the spinal nerves are formed exclusively of motor fibres; the posterior roots exclusively of sensory fibres. Beyond the ganglia, all the spinal nerves are mixed nerves, and contain as well sympathetic filaments.

The Sympathetic Nerve.

The general differences between the fibres of the cerebro-spinal and sympathetic nerves have been already stated (pp. 544, 545), but the different modes of action of the two systems cannot be referred to the different structure of their fibres. It is probable, however, that the laws of conduction by the fibres are in both systems the same, and that the differences manifest in the modes of action of the systems are due to the multiplication and separation of the nervous centres of the sympathetic: ganglia, or nerve-centres, being placed in connection with the fibres of the sympathetic in nearly all parts of their course.

Distribution.—1. Fibres are distributed to all plain or unstriped muscular fibres, as those of the blood-vessels (vaso-motor nerves), of the muscular coats of the intestines and other hollow viscera, of gland-ducts, of the iris and ciliary muscle in the eye, and elsewhere.

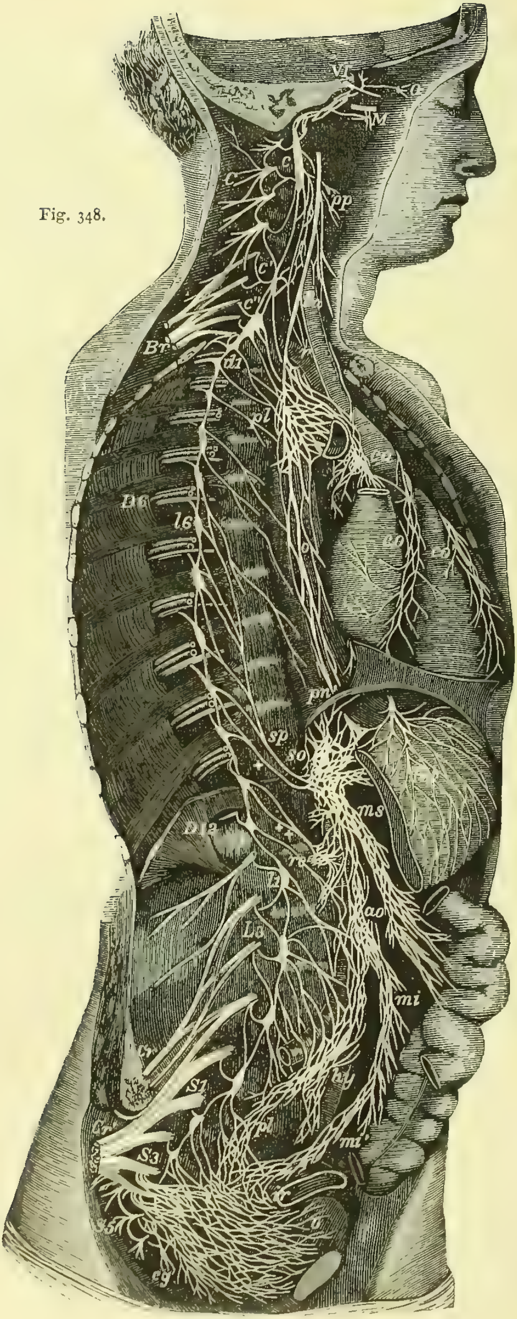
The vaso-motor fibres come originally from the *vaso-motor centre* in the medulla oblongata; and, issuing from the spinal cord, communicate with the præ-vertebral chain of ganglia, and are thence, as branches from these, distributed to the Blood-vessels. 2. Fibres (accelerating) are distributed to the Heart. 3. Secretory fibres (in addition to vaso-motor) are distributed to the salivary, and presumably to other secreting glands. 4. Inter-central or inter-ganglionic fibres. 5. *Centripetal* fibres proceeding to the vaso-motor centre in the medulla; to the various sympathetic ganglia; and probably to all cerebro-spinal nerve-centres. The *peripheral* distribution of these centripetal fibres is, without doubt, chiefly in the parts or organs to which the *centrifugal* fibres of the same system are mainly distributed. But they are also present in all those other parts of the body which belong more especially to the Cerebro-spinal system.

Structure.—The sympathetic ganglia all contain—(1), nerve-fibres traversing them; (2), nerve-fibres originating in them; (3), nerve- or ganglion-corpuscles, giving origin to these fibres; and (4), other corpuscles that appear free. In the sympathetic ganglia of the frog, ganglion-cells of a very complicated structure have been described by Beale and subsequently by Arnold. The cells are enclosed each in a nucleated capsule: they are pyriform in shape, and from the pointed end two fibres are given off, which gradually acquire the characters of nerve-fibres: one of them is straight, and the other (which sometimes arises from the cell by two roots) is spirally coiled around it.

In the trunk, and thence proceeding branches of the sympathetic, there appear to be always—(1), fibres which arise in its own ganglia; (2), fibres derived from the ganglia of the cerebral and spinal nerves; (3), fibres derived from the brain and spinal cord and transmitted through the roots of their nerves. The spinal cord, indeed, appears to be a large source of the fibres of the sympathetic nerve.

Through the communicating branches between the spinal nerves and the præ-vertebral sympathetic ganglia, which have been generally called roots or origins of the sympathetic nerve, an interchange is effected between all the spinal nerves and the

Fig. 348.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sympathetic trunks; all the ganglia, also, which are seated on the cerebral nerves, have roots (as they are called) through which filaments of the cerebral nerves are added to their own. So that, probably, all sympathetic nerves contain some intermingled cerebral or spinal nerve-fibres; and all cerebral and spinal nerves some filaments derived from the sympathetic system or from ganglia. But the proportions in which these filaments are mingled are not uniform. The nerves which arise from the brain and spinal cord retain throughout their course and distribution a preponderance of *cerebro-spinal* fibres, while the nerves immediately arising from the so-called sympathetic ganglia probably contain a majority of *sympathetic* fibres. But inasmuch as there is no certainty that in structure the branches of cerebral or spinal nerves differ always from those of the sympathetic system, it is

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Fig. 348.—*Diagrammatic view of the Sympathetic cord of the right side*, showing its connections with the principal cerebro-spinal nerves and the main præaortic plexuses. ¼. (From Quain's Anatomy.)

Cerebro-spinal nerves.—VI, a portion of the sixth cranial as it passes through the cavernous sinus, receiving two twigs from the carotid plexus of the sympathetic nerve; O, ophthalmic ganglion connected by a twig with the carotid plexus; M, connection of the spheno-palatine ganglion by the Vidian nerve with the carotid plexus; C, cervical plexus; Br, brachial plexus; D 6, sixth intercostal nerve; D 12, twelfth; L 3, third lumbar nerve; S 1, first sacral nerve; S 3, third; S 5, fifth; Cr, anterior crural nerve; Cr′, great sciatic; *pn*, pneumogastric nerve in the lower part of the neck; *r*, recurrent nerve winding round the subclavian artery.

Sympathetic Cord.—*c*, superior cervical ganglion; *c′*, second or middle; *c″*, inferior: from each of these ganglia cardiac nerves (all deep on this side) are seen descending to the cardiac plexus; *d* 1, placed immediately below the first dorsal sympathetic ganglion; *d* 6, is opposite the sixth; *l* 1, first lumbar ganglion; *c g*, the terminal or coccygeal ganglion.

Præaortic and Visceral Plexuses.—*p p*, pharyngeal, and, lower down, laryngeal plexus; *pl*, posterior pulmonary plexus spreading from the vagus on the back of the right bronchus; *c a*, on the aorta, the cardiac plexus, towards which, in addition to the cardiac nerves from the three cervical sympathetic ganglia, other branches are seen descending from the vagus and recurrent nerves; *co*, right or posterior, and *co′*, left or anterior coronary plexus; *o*, œsophageal plexus in long meshes on the gullet; *sp*, great splanchnic nerve formed by branches from the fifth, sixth, seventh, eighth, and ninth dorsal ganglia; +, small splanchnic from the ninth and tenth; + +, smallest or third splanchnic from the eleventh: the first and second of these are shown joining the solar plexus, *s o;* the third descending to the renal plexus, *r e*; connecting branches between the solar plexus and the vagi are also represented; *pn′*, above the place where the right vagus passes to the lower or posterior surface of the stomach; *pn″*, the left distributed on the anterior or upper surface of the cardiac portion of the organ: from the solar plexus large branches are seen surrounding the arteries of the cœliac axis, and descending to *m s*, the superior mesenteric plexus; opposite to this is an indication of the suprarenal plexus; below *r e* (the renal plexus), the spermatic plexus is also indicated; *a o*, on the front of the aorta, marks the aortic plexus, formed by nerves descending from the solar and superior mesenteric plexuses and from the lumbar ganglia; *mi*, the inferior mesenteric plexus surrounding the corresponding artery; *hy*, hypogastric plexus placed between the common iliac vessels, connected above with the aortic plexus, receiving nerves from the lower lumbar ganglia, and dividing below into the right and left pelvic or inferior hypogastric plexuses; *pl*, the right pelvic plexus; from this the nerves descending are joined by those from the plexus on the superior hemorrhoidal vessels, *mi′*, by sympathetic nerves from the sacral ganglia, and by numerous visceral nerves from the third and fourth sacral spinal nerves, and there are thus formed the rectal, vesical, and other plexuses, which ramify upon the viscera from behind forwards and from below upwards, as towards *ir*, and *v*, the rectum and bladder.

impossible in the present state of our knowledge to be sure of the source of fibres which from their structure might lead the observer to believe that they arose from the brain or spinal cord on the one hand, or from the sympathetic ganglia on the other. In other words, although the large white medullated fibres are especially characteristic of cerebro-spinal nerves, and the pale or non-medullated fibres of a sympathetic nerve, in which they largely preponderate, there is no certainty to be obtained in a doubtful case, of whether the nerve-fibre is derived from one or the other, from mere examination of its structure. It may be derived from either source.

Functions.—It may be stated generally that the sympathetic nerve-fibres are simple conductors of impressions, as are those of the Cerebro-spinal system; and that the ganglionic centres have (each in its appropriate sphere) the like powers both of *conducting*, *transferring*, *reflecting*, and possibly of *augmenting* or of *inhibiting* impressions made on them.

The power possessed by the sympathetic ganglia of conducting impressions is sufficiently proved in disease, as when any of the viscera, usually unfelt, give rise to sensations of pain, or when a part not commonly subject to mental influence is excited or retarded in its actions by the various conditions of the mind; for in all these cases impressions must be conducted to and fro through the whole distance between the part and the spinal cord and brain. So, also, in experiments, now more than sufficiently numerous, irritations of the semilunar ganglia, the splanchnic nerves, the thoracic, hepatic, and other ganglia and nerves, have elicited expressions of pain, and have excited movements in the muscular organs supplied from the irritated part.

In the case of pain, or of movements affected by mental conditions, it may be supposed that the conduction of impressions is effected through the cerebro-spinal fibres which are mingled in all, or nearly all, parts of the sympathetic nerves. There are no means of deciding this; but if it be admitted that the conduction is effected through the cerebro-spinal nerve-fibres, then, whether or not they pass uninterruptedly between the brain or spinal cord and the part affected, it must be assumed that their mode of conduction is modified by the ganglia. For, if such cerebro-spinal fibres are conducted in the ordinary manner, the parts should be always sensible and liable to the influence of the will, and impressions should be conveyed to and fro instantaneously. But this is not the case; on the contrary, through the branches of the sympathetic nerve and its ganglia, none but intense impressions, or impressions exaggerated by the morbid excitability of the nerves or ganglia, can be conveyed.

Respecting the general action of the ganglia of the sympathetic nerve, in reflex or other actions, little need be said here, since they may be taken as examples by which to illustrate the common modes of action of all nerve-centres (see p. 558). Indeed, complex as the sympathetic system, taken as a whole, is, it presents in each of its parts a simplicity not to be found in the cerebro-spinal system: for each ganglion with afferent and efferent nerves forms a simple nervous system, and might serve for the illustration of all the nervous actions with which the mind is unconnected.

The parts principally supplied with sympathetic nerves are usually capable of none but involuntary movements, and when the mind acts on them at all, it is only through the strong excitement or depressing influence of some passion, or through some voluntary movement with which the actions of the involuntary part are commonly associated. The heart, stomach, and intestines are examples of these statements; for the heart and stomach, though supplied in large measure from the pneumogastric nerves, yet probably derive through them few filaments except such as have arisen from their ganglia, and are therefore of the nature of sympathetic fibres.

The parts which are supplied with motor power by the sympathetic nerve continue to move, though more feebly than before, when they are separated from their natural connections with the rest of the sympathetic system, and wholly removed from the body. Thus, the heart, after it is taken from the body, continues to beat in Mammalia for one or two minutes, in reptiles and Amphibia for hours; and the peristaltic motions of the intestine continue under the same circumstances. Hence the motions of the parts supplied with nerves from the sympathetic are shown to be, in a measure, independent of the brain and spinal cord; this independent maintenance of their action being, without duobt, due to the fact that they contain, in their own substance, the apparatus of ganglia and nerve-fibres by which their motions are immediately governed.

It seems to be a general rule, at least in animals that have both cerebro-spinal and sympathetic nerves much developed, that the involuntary movements excited by stimuli conveyed through ganglia are orderly and like natural movements, while those excited through nerves without ganglia are convulsive and disorderly; and the probability is that, in the natural state, it is through the same ganglia that natural stimuli, impressing centripetal nerves, are reflected through centrifugal nerves to the involuntary muscles. As the muscles of respiration are maintained in uniform rhythmic action chiefly by the reflecting and combining power of the medulla oblongata, so are those of the heart, stomach, and intestines, by their several ganglia. And as with the ganglia of the sympathetic and their nerves, so with the medulla oblongata and its nerves distributed to the respiratory muscles,—if these nerves of the medulla oblongata itself be directly stimulated, the movements that follow are convulsive and disorderly; but if the medulla be stimulated through a centripetal nerve, as when cold is applied to the skin, then the impressions are reflected so as to produce movements which, though they may be very quick and almost convulsive, are yet combined in the plan of the proper respiratory acts.

Among the ganglia of the sympathetic nerves to which this co-ordination of movements is to be ascribed, must be reckoned, not those alone which are on the principal trunks and branches of the sympathetic external to any organ, but those also which lie in the very substance of the organs; such as those of the heart (p. 155). Those also may be included which have been found in the mesentery close by the intestines, as well as in the muscular and sub-mucous tissue of the stomach and intestinal canal (pp. 302, 315), and in other parts. The extension of discoveries of such ganglia will probably diminish yet further the number of instances in which the involuntary movements appear to be effected independently of nervous influence.

Respecting the influence of the sympathetic system on various physiological processes, see Heart (p. 158), Arteries (p. 190), Animal Heat (p. 391), Salivary Glands (p. 287), Stomach (p. 312), Intestines (p. 316). These are parts which have been specially investigated. But they are not in any way exceptional. All physiological processes must, of necessity, either directly or through vaso-motor fibres, be under the influence of the Sympathetic system.

Influence of the Nervous System on Nutrition.—It has been held that the nervous system cannot be essential to a healthy course of nutrition, because in plants and the early embryo, and in the lowest animals, in which no nervous system is developed, nutrition goes on without it. But this is no proof that in animals which have a nervous system, nutrition may be independent of it; rather, it may be assumed, that in ascending development, as one system after another is added or increased, so the highest (and, highest of all, the nervous system) will always be inserted and blended in a more and more intimate relation with all the rest: according to the general law, that the interdependence of parts augments with their development.

The reasonableness of this assumption is proved by many facts showing the influence of the nervous system on nutrition, and by the most striking of these facts being observed in the higher animals, and especially in man. The influence of the mind in the production, aggravation, and cure of organic diseases is matter of daily observation, and a sufficient proof of influence exercised on nutrition through the nervous system.

Independently of mental influence, injuries either to portions of the nervous centres, or to individual nerves, are frequently followed by defective nutrition of the parts supplied by the injured nerves, or deriving their nervous influence from the damaged portions of the nervous centres. Thus, lesions of the spinal cord are sometimes followed by mortification of portions of the paralysed parts; and this may take place very quickly, as in a case in which the ankle sloughed within twenty-four hours after an injury of the spine. After such lesions also, the repair of injuries in the paralysed parts may take place less completely than in others; so, in a case in which paraplegia was produced by fracture of the lumbar vertebræ, and, in the same accident, the humerus and tibia were fractured. The former in due time united: the latter did not. The same fact was illustrated by some experiments, in which having, in salamanders, cut off the end of the tail, and then thrust a thin wire some distance up the spinal canal, so as to destroy the cord, it was found that the end of the tail was reproduced more slowly than in other salamanders in whom the spinal cord was left uninjured above the point at which the tail was amputated. Illustrations of the same kind are furnished by the several cases in which division or destruction of the trunk of the trigeminal nerve has been followed by incomplete and morbid nutrition of the corresponding side of the face ; ulceration of the cornea being often directly or indirectly one of the consequences of such imperfect nutrition. Part of the wasting and slow degeneration of tissue in paralysed limbs is probably referable also to the withdrawal of nervous influence from them ; though, perhaps, more is due to the want of use of the tissues.

Undue irritation of the trunks of nerves, as well as their division or destruction, is sometimes followed by defective or morbid nutrition. To this may be referred the cases in which ulceration of the parts supplied by the irritated nerves occurs frequently, and continues so long as the irritation lasts. Further evidence of the influence of the nervous system upon nutrition is furnished by those cases in which, from mental anguish, or in severe neuralgic headaches, the hair becomes grey very quickly, or even in a few hours.

So many and varied facts leave little doubt that the nervous system exercises an influence over nutrition as over other organic processes ; and they cannot be easily explained by supposing that the changes in the nutritive processes are only due to the variations in the size of the blood-vessels supplying the affected parts, although this is, doubtless, one important element in producing the result.

The question remains, through what class of nerves is the influence exerted ? When defective nutrition occurs in parts rendered inactive by injury of the motor nerve alone, as in the muscles and other tissues of a paralysed face or limb, it may appear as if the atrophy were the direct consequence of the loss of power in the motor nerves ; but it is more probable that the atrophy is the consequence of the want of exercise of the parts ; for if the muscles be exercised by artificial irritation of their nerves their nutrition will be less defective. The defect of the nutritive process which ensues in the face and other parts, however, in consequence of destruction of the trigeminal nerve, cannot be referred to loss of influence of any motor nerves; for the motor-nerves of the face and eye, as well as the olfactory and optic, have no share in the defective nutrition which follows injury of the trigeminal nerve; and one or all of them may be destroyed without any direct disturbance of the nutrition of the parts they severally supply.

It must be concluded, therefore, that the influence which is exercised by nerves over the nutrition of parts to which they are distributed is to be referred, in part or altogether, either to the nerves of common sensation, or to the vaso-motor nerves, or, as it is by some supposed, to nerve-fibres (*trophic* nerves), which preside specially over the nutrition of the tissues and organs to which they are supplied.

It is not at present possible to say whether the influence on nutrition is exercised through the cerebro-spinal or through the sympathetic nerves, which, in the parts on which the observation has been made, are generally combined in the same sheath. The truth perhaps is, that it may be exerted through either or both of these nerves. The defect of nutrition which ensues after lesion of the spinal cord alone, the sympathetic nerves being uninjured, and the general atrophy which sometimes occurs in consequence of diseases of the brain, seem to prove the influence of the cerebro-spinal system: while the observation that inflammation of the eye is a constant result of ligature of the sympathetic nerve in the neck, and many other observations of a similar kind, exhibit very well the influence of the latter nerve in nutrition.

CHAPTER XIX.

THE SENSES.

THROUGH the medium of the Nervous system the mind obtains a knowledge of the existence both of the various parts of the body, and of the external world. This knowledge is based upon *sensations* resulting from the stimulation of certain centres in the brain, by irritations conveyed to them by afferent (sensory) nerves. Under normal circumstances, the following structures are necessary for sensation: (*a*) A peripheral organ for the reception of the impression; (*b*) a nerve for conducting it; (*c*) a nerve-centre for feeling or perceiving it.

Classification of Sensations.—Sensations may be conveniently classed as (1) *common* and (2) *special.*

(1.) *Common sensations.*—Under this head fall all those general sensations which cannot be distinctly localized in any particular part of the body, such as Fatigue, Discomfort, Faintness, Satiety, together with Hunger and Thirst, in which, in addition to a general discomfort, there is in many persons a distinct sensation referred to the stomach or fauces. In this class must also be placed the various irritations of the mucous membrane of the bronchi, which give rise to coughing, and also the sensations derived from various viscera indicating the necessity of expelling their contents; *e.g.*, the desire to defæcate, to urinate, and, in the female, the sensations which precede the expulsion of the fœtus. We must also include such sensations as itching, creeping, tickling, tingling, burning, aching, etc., some of which come under the head of *pain:* they will be again referred to in describing the sense of *Touch.* It is impossible to draw a very clear line of demarcation between many of the common sensations above mentioned, and the sense of Touch, which forms the connecting link between the general and special sensations. Touch is, indeed, usually classed with the special senses, and will be considered in the same group with them; yet it differs from them in being common to many nerves; *e.g.*, all the sensory spinal nerves, the vagus, glosso-pharyngeal, and fifth cerebral nerves, and in its impressions being communicable through many organs. Among common sensations must also be ranked the *muscular sense*, which has been already alluded to. It is by means of this sense that we become aware of the condition of contraction or relaxation of the various muscles and groups of muscles, and thus obtain the information necessary for their adjustment to various purposes—standing, walking, grasping, etc. This muscular sensibility is shown in our power to estimate the differences between weights by the different muscular efforts necessary to raise them. Considerable delicacy may be attained by practice, and the difference between 19½ oz. in one hand and 20 oz. in the other is readily appreciated (Weber).

This sensibility with which the muscles are endowed must be carefully distinguished from the sense of *contact* and of *pressure*, of which the skin is the organ. When standing erect, we can feel the ground (contact), and further there is a sense of *pressure*, due to our feet being pressed against the ground by the weight of the body. Both these are derived from the skin of the sole of the foot. If now we raise the body on the toes, we are conscious (muscular sense) of a muscular effort made by the muscles of the calf, which overcomes a certain resistance.

(2.) *Special Sensations.*—Including the sense of touch, the special senses are five in number—Touch, Taste, Smell, Hearing, Sight.

Difference between Common and Special Sensations.—The most important distinction between common and special sensations is that by the former we are made aware of certain conditions of various parts of our bodies, while from the latter we gain our knowledge of the external world also. This difference will be clear if we compare the sensations of pain and touch, the former of which is a common, the latter a special sensation. "If we place the edge of a sharp knife on the skin, we feel the edge by means of our sense of touch; we perceive a sensation, and refer it to the object which has caused it. But as soon as we cut the skin with the knife, we feel pain, a feeling which we no longer refer to the cutting knife, but which we feel within ourselves, and which communicates to us the fact of a change of condition in our own body. By the sensation of pain we are neither able to recognise the object which caused it, nor its nature" (Weber).

General Characteristics: Seat.—In studying the phenomena of sensation, it is important clearly to understand that the *Sensorium*, or seat of sensation, is in the Brain, and not in the particular organ (eye, ear, etc.) through which the sensory impression is received. In common parlance we are said to *see* with the eye, *hear* with the ear, etc., but in reality these organs are only adapted to receive impressions which are conducted to the sensorium, through the optic and auditory nerves respectively, and there give rise to sensation.

Hence, if the optic nerve is severed (although the eye itself is perfectly uninjured), vision is no longer possible; since, although the image falls on the retina as before, the sensory impression can no longer be conveyed to the sensorium. When any given sensation is felt, all that we can with certainty affirm is that the sensorium in the brain is excited. The exciting cause may be (in the vast majority of cases is), some object of the external world (*objective sensation*); or the condition of the sensorium may be due to some excitement within the brain, in which case the sensation is termed *subjective*. The mind habitually refers sensations to external causes; and hence, whenever they are subjective (due to causes within the brain), we can hardly divest ourselves of the idea of an external cause, and an *illusion* is the result.

Illusions.—Numberless examples of such illusions might be quoted. As familiar cases may be mentioned, humming and buzzing in the ears caused by some irritation of the auditory nerve or centre, and even musical sounds and voices (sometimes termed auditory spectra); also so-called optical illusions: persons and other objects are described as being seen, although not present. Such illusions are most strikingly exemplified in cases of delirium tremens or other forms of delirium, in which cats, rats, creeping loathsome forms, etc., are described by the patient as seen with great vividness.

Causes of Illusions.—One uniform *internal* cause, which may act on all the nerves of the senses in the same manner, is the accumulation of blood in their capillary vessels, as in congestion and inflammation. This one cause excites in the retina, while the eyes are closed, the sensations of light and luminous flashes; in the auditory nerve, the sensation of humming and ringing sounds; in the olfactory nerve, the sense of odours; and in the nerves of feeling, the sensation of pain. In the same way, also, a narcotic substance, introduced into the blood, excites in the nerves of each sense peculiar symptoms: in the optic nerves, the appearance of luminous sparks before the eyes; in the auditory nerves, "tinnitus aurium"; and in the common sensory nerves, the sensation of creeping over the surface. So, also, among *external* causes, the stimulus of electricity, or the mechanical influence of a blow, concussion, or pressure, excites in the eye the sensation of light and colours; in the ear, a sense of a loud sound or of ringing; in the tongue, a saline or acid taste; and in the other parts of the body, a perception of peculiar jarring or of the mechanical impression, or a shock like it.

Sensations and Perceptions.—The habit of constantly referring our sensations to external causes, leads us to interpret the various modifications which external objects produce in our sensations, as *properties* of the external bodies themselves. Thus we speak of certain substances as possessing a disagreeable taste and smell; whereas, the fact is, their taste and smell are only disagreeable to *us.* It is evident, however, that on this habit of referring our sensations to causes outside ourselves (perception), depends the reality of the external world to us; and more especially is this the case with the senses of touch and sight. By the co-operation of these two senses aided by the others, we are enabled gradually to attain a knowledge of external objects which daily experience confirms, until we come to place unbounded confidence in what is termed the "evidence of the senses."

Judgments.—We must draw a distinction between mere sensations, and the judgments based, often unconsciously, upon them. Thus, in looking at a near object, we unconsciously estimate its distance, and say it seems to be ten or twelve feet off: but the estimate of its distance is in reality a *judgment* based on many things besides the appearance of the object itself; among which may be mentioned the number of intervening objects, the number of steps which from past experience we know we must take before we could touch it, and many others.

Symptoms of Irritation of Nerves of Special Sense.—Irritation of the optic nerve, as by cutting it, invariably produces a sensation of light, of the auditory nerve a sensation of some modification of sound. Doubtless these distinct sensations depend not on any speciality in the structure of the nerves of special sense, but on the nature of their connections in the sensorium.

Experiments seem to have proved that none of these nerves possess the faculty of common sensibility. Thus, Magendie observed that when the olfactory nerves, laid bare in a dog, were pricked, no signs of pain were manifested; and other experiments of his seem to show that both the retina and optic nerve are insusceptible of pain. Further, the optic nerve is insusceptible to the stimulus of light when severed from its connection with the retina, which alone is adapted to receive luminous impressions.

Sensation of Motion is, like motion itself, of two kinds,—progressive and vibratory. The faculty of the perception of progressive motion is possessed chiefly by the senses of vision, touch, and taste. Thus an impression is perceived travelling from one part of the retina to another, and the movement of the image is interpreted by the mind as the motion of the object. The same is the case in the sense of touch; so also the movement of a sensation of taste over the surface of the organ of taste, can be recognised. The motion of tremors, or vibrations, is perceived by several senses, but especially by those of hearing and touch.

Sensations of Chemical Actions.—We are made acquainted with *chemical actions* principally by taste, smell, and touch, and by each of these senses in the mode proper to it. Volatile bodies, disturbing the conditions of the nerves by a chemical action, exert the greatest influence upon the organ of smell; and many matters act on that sense which produce no impression upon the organs of taste and touch,—for example, many odorous substances, as the vapour of metals, such as lead, and the vapour of many minerals. Some volatile substances, however, are perceived not only by the sense of smell, but also by the senses of touch and taste. Thus, the vapours of horse-radish and mustard, and acrid suffocating gases, act upon the conjunctiva and the mucous membrane of the lungs, exciting, through the common sensory nerves, merely modifications of common feeling; and at the same time they excite the sensations of smell and of taste.

Special Senses—Touch.

Seat.—The sense of touch is not confined to particular parts of the body of small extent, like the other senses; on the contrary, all parts capable of perceiving the presence of a stimulus by ordinary sensation are, in certain degrees, the seat of this sense; for touch is simply a modification or exaltation of common sensation or sensibility. The nerves on which the sense of touch depends are, therefore, the same as those which confer ordinary sensation on the different parts of the body, viz., those derived from the posterior roots of the nerves of the spinal cord, and the sensory cerebral nerves.

But, although all parts of the body supplied with sensory nerves are thus, in some degree, organs of touch, yet the sense is exercised in perfection only in those parts the sensibility of which is extremely delicate, *e.g.*, the skin, the tongue, and the lips, which are provided with abundant papillæ. A peculiar and, of its own kind in each case, a very acute sense of touch is exercised through the medium of the nails and teeth. To a less extent the hair may be reckoned an organ of touch; as in the case of the eyelashes. The sense of touch renders us conscious of the presence of a stimulus, from the slightest to the most intense degree of its action, by that indescribable something which we call feeling, or common sensation. The modifications of this sense often depend on the extent of the parts affected. The sensation of pricking, for example, informs us that the sensitive particles are intensely affected in a small extent; the sensation of pressure indicates a slighter affection of the parts in the greater extent, and to a greater depth. It is by the depth to which the parts are affected that the feeling of pressure is distinguished from that of mere contact. Schiff and Brown-Séquard are of opinion that common sensibility and tactile sensibility manifest themselves to the individual by the aid of different sets of fibres. Sieveking has arrived at the same conclusion from pathological observation.

Varieties.—(*a*) The sense of *touch*, strictly so-called (tactile sensibility), (*b*) the sense of *pressure*, (*c*) the sense of *temperature*. These when carried beyond a certain degree are merged in (*d*) the sensation of *pain*.

Various peculiar sensations, such as *tickling*, must be classed with pain under the head of common sensations, since they give us no information as to external objects. Such sensations, whether pleasurable or painful, are in all cases referred by the mind to the part affected, and not to the cause which stimulates the sensory nerves of the part. The sensation of tickling may be produced in many parts of the body, but with especial intensity in the soles of the feet. Among other sensations belonging to this class, and confined to particular parts of the body, may be mentioned those of the genital organs and nipples.

(*a*) **Touch proper.**—In almost all parts of the body which have delicate tactile sensibility the epidermis, immediately over the papillæ, is moderately thin. When its thickness is much increased, as over the heel, the sense of touch is very much dulled. On the other hand, when it is altogether removed, and the cutis laid bare, the sensation of contact is replaced by one of pain. Further, in all highly sensitive parts, the papillæ are numerous and highly vascular, and usually the sensory nerves are connected with special End-organs, such as have been described (p. 415).

The acuteness of the sense of touch depends very largely on the cutaneous circulation, which is of course largely influenced by external temperature. Hence the numbness, familiar to everyone, produced by the application of cold to the skin.

Special organs of touch are present in most animals, among which may be mentioned the antennæ of insects, the "whiskers" (vibrissæ) of cats and other carnivora, the wings of bats, the trunk of the elephant, and the hand of man.

Judgment of the Form and Size of Bodies.—By the sense of touch the mind is made acquainted with the size, form, and other external characters of bodies. And in order that these characters may be easily ascertained, the sense of touch is especially developed in those parts which can be readily moved over the surface of bodies. Touch, in its more limited sense, or the act of examining a body by the touch, consists merely in a voluntary employment of this sense combined with movement, and stands in the same relation to the sense of touch, or common sensibility, generally, as the act of seeking, following, or examining odours, does to the sense of smell. The hand is best adapted for it, by reason of its peculiarities of structure,—namely, its capability of pronation and supination, which enables it, by the movement of rotation, to examine the whole circumference of the body; the power it possesses of opposing the thumb to the rest of the hand, and the relative mobility of the fingers; and lastly from the abundance of the sensory terminal organs which it possesses. In forming a conception of the figure and extent of a surface, the mind multiplies the size of the hand or fingers used in the inquiry by the number of times which it is contained in the surface traversed; and by repeating this process with regard to the different dimensions of a solid body, acquires a notion of its cubical extent, but, of course, only an imperfect notion, as other senses, *e.g.*, the sight, are required to make it complete.

Acuteness of Touch.—The perfection of the sense of touch on different parts of the surface is proportioned to the power which such parts possess of distinguishing and isolating the sensations produced by two points placed close together. This power depends, at least in part, on the number of primitive nerve-fibres distributed to the part; for the fewer the primitive fibres which an organ receives, the more likely is it that several impressions on different contiguous points will act on only one nervous fibre, and hence be confounded, and perhaps produce but one sensation. Experiments have been made to determine the tactile properties of different parts of the skin, as measured by this power of distinguishing distances. These consist in touching the skin, while the eyes are closed, with the points of a pair of compasses sheathed with cork, and in ascertaining how close the points of compasses might be brought to each other, and still be felt as two bodies. (E. H. Weber, Valentin.)

Table of variations in the tactile sensibility of different parts.—*The measurement indicates the least distance at which the two blunted points of a pair of compasses could be separately distinguished.* (E. H. Weber.)

Tip of tongue	$\frac{1}{24}$	inch
Palmar surface of third phalanx of forefinger	$\frac{1}{12}$	
Palmar surface of second phalanges of fingers	$\frac{1}{6}$	„
Red surface of under-lip . . .	$\frac{1}{6}$	
Tip of the nose	$\frac{1}{4}$	„

Middle of dorsum of tongue	$\frac{1}{3}$	inch.
Palm of hand	$\frac{5}{12}$	,,
Centre of hard palate	$\frac{1}{2}$	,,
Dorsal surface of first phalanges of fingers	$\frac{7}{12}$	,,
Back of hand	$1\frac{1}{6}$	,,
Dorsum of foot near toes	$1\frac{1}{2}$	,,
Gluteal region	$1\frac{1}{2}$	,,
Sacral region	$1\frac{1}{2}$	,,
Upper and lower parts of forearm	$1\frac{1}{2}$	,,
Back of neck near occiput	2	,,
Upper dorsal and mid-lumbar regions	2	,,
Middle part of forearm	$2\frac{1}{2}$	,,
Middle of thigh	$2\frac{1}{2}$	,,
Mid-cervical region	$2\frac{1}{2}$	,,
Mid-dorsal region	$2\frac{1}{2}$	,,

Moreover, in the case of the limbs, it was found that before they were recognised as two, the points of the compasses had to be *further* separated when the line joining them was in the long axis of the limb, than when in the transverse direction.

According to Weber the mind estimates the distance between two points by the number of unexcited nerve-endings which intervene between the two points touched. It would appear that a certain number of intervening unexcited nerve-endings are necessary before two points touched can be recognised as separate, and the greater this number the more clearly are the points of contact distinguished as separate. By practice the delicacy of a sense of touch may be very much increased. A familiar illustration occurs in the case of the blind, who, by constant practice, can acquire the power of reading raised letters the forms of which are almost if not quite undistinguishable, by the sense of touch, to an ordinary person.

The power of correctly localising sensations of touch is gradually derived from experience. Thus infants when in pain simply cry, but make no effort to remove the cause of irritation, as an older child or adult would, doubtless on account of their imperfect knowledge of its exact situation. By long experience this power of localisation becomes perfected, till at length the brain possesses a complete "picture" as it were of the surface of the body, and is able with marvellous exactness to localise each sensation of touch.

Illusions of Touch.—The different degrees of sensitiveness possessed by different parts may give rise to errors of judgment in estimating the distance between two points where the skin is touched. Thus, if blunted points of a pair of compasses (maintained at a constant distance apart) be slowly drawn over the skin of the cheek towards the lips, it is almost impossible to resist the conclusion that the distance between the points is gradually increasing. When they reach the lips they seem to be considerably further apart than on the cheek. Thus, too, our estimate of the size of a cavity in a tooth is usually exaggerated when based upon sensation derived from the tongue alone. Another curious illusion may here be mentioned. If we close the eyes, and place a small marble or pea between the crossed fore and middle fingers, we seem to be touching two marbles. This illusion is due to an error of judgment. The marble is touched by two surfaces which, under ordinary circumstances, could only be touched by two separate marbles, hence the mind, taking no cognizance of the fact that the fingers are crossed, forms the conclusion that two sensations are due to two marbles.

(*b*) **Pressure.**—It is extremely difficult to separate touch proper from sensations of pressure, and, indeed, the former may be said to depend upon the latter. If the hand be rested on the table and a very light body such as a small card placed on it, the only sensation produced is one of contact ; if, however, an ounce weight be laid on the card an additional sensation (that of pressure) is experienced, and this becomes more intense as the weight is increased. If now the weight be raised by the hand, we are conscious of overcoming a certain resistance ; this consciousness is due to what is termed the "*muscular sense*" (p. 599). The estimate of a weight is, therefore, usually based on *two* sensations, (1) of pressure on the skin, and (2) the muscular sense.

The estimate of weight derived from a combination of these two sensations (as in lifting a weight) is more accurate than that derived from the former alone (as when a weight is laid on the hand) ; thus Weber found that by the former method he could generally distinguish 19½ oz. from 20 oz., but not 19¾ oz. from 20 oz., while by the latter he could at most only distinguish 14½ oz. from 15 oz.

It is not the absolute, but the relative, amount of the difference of weight which we have thus the faculty of perceiving.

It is not, however, certain, that our idea of the amount of muscular force used is derived solely from sensation in the muscles. We have the power of estimating very accurately beforehand, and of regulating, the amount of nervous influence necessary for the production of a certain degree of movement. When we raise a vessel, with the contents of which we are not acquainted, the force we employ is determined by the idea we have conceived of its weight. If it should happen to contain some very heavy substance, as quicksilver, we shall probably let it fall ; the amount of muscular action, or of nervous energy, which we had exerted being insufficient. The same thing occurs sometimes to a person descending stairs in the dark ; he makes the movement for the descent of a step which does not exist. It is possible that in the same way the idea of weight and pressure in raising bodies, or in resisting forces, may in part arise from a consciousness of the amount of nervous energy transmitted from the brain rather than from a sensation in the muscles themselves. The mental conviction of the inability longer to support a weight must also be distinguished from the actual sensation of fatigue in the muscles.

So, with regard to the ideas derived from sensations of touch combined with movements, it is doubtful how far the consciousness of the extent of muscular movement is obtained from sensations in the muscles themselves. The sensation of movement attending the motions of the hand is very slight; and persons who do not know that the action of particular muscles is necessary for the production of given movements, do not suspect that the movement of the fingers, for example, depends on an action in the forearm. The mind has, nevertheless, a very definite knowledge of the changes of position produced by movements ; and it is on this that the ideas which it conceives of the extension and form of a body are in great measure founded.

(*c*) **Temperature.**—The whole surface of the body is more or less sensitive to differences of temperature. The sensation of heat is distinct from that of touch ; and it would seem reasonable to suppose that there are special nerves and nerve-endings for temperature. At any rate the power of discriminating temperature may remain unimpaired when the sense of touch is temporarily in abeyance. Thus if the ulnar nerve be compressed at the elbow till the sense of touch is very much dulled in the fingers which it supplies, the sense of temperature remains quite unaffected (Nothnagel).

The sensations of heat and cold are often exceedingly fallacious, and in many cases are no guide at all to the absolute temperature as indicated by a thermometer. All that we can with safety infer from our sensations of temperature, is that a given object is warmer or cooler than the skin. Thus the temperature of our skin is the standard; and as this varies from hour to hour according to the activity of the cutaneous circulation, our estimate of the absolute temperature of any body must necessarily vary too. If we put the left hand into water at 40° F. and the right into water at 110° F., and then immerse both in water at 80° F., it will feel warm to the left hand but cool to the right. Again a piece of metal which has really the same temperature as a given piece of wood will feel much colder, since it conducts away the heat much more rapidly. For the same reason air in motion feels very much cooler than air of the same temperature at rest.

Perhaps the most striking example of the fallaciousness of our sensations as a measure of temperature is afforded by fever. In a shivering fit of ague the patient feels excessively cold, whereas his actual temperature is several degrees above the normal, while in the sweating stage which succeeds it he feels very warm, whereas really his temperature has fallen several degrees. In the former case the cutaneous circulation is much diminished, in the latter much increased; hence the sensations of cold and heat respectively.

In some cases we are able to form a fairly accurate estimate of absolute temperature. Thus, by plunging the elbow into a bath, a practised bath-attendant can tell the temperature sometimes within 1° F.

The temperatures which can be readily discriminated are between 50°—115° F. (10°—45° C.); very low and very high temperature alike produce a burning sensation. A temperature appears higher according to the extent of cutaneous surface exposed to it. Thus, water of a temperature which can be readily borne by the hand, is quite intolerable if the whole body be immersed. So, too, water appears much hotter to the hand than to a single finger.

The delicacy of the sense of temperature coincides in the main with that of touch, and appears to depend largely on the thickness of the skin; hence, in the elbow where the skin is thin, the sense of temperature is delicate, though that of touch is not remarkably so. Weber has further ascertained the following facts: two compass points so near together on the skin that they produce but a single impression, at once give rise to *two* sensations, when one is hotter than the other. Moreover, of two bodies of equal weight, that which is the colder feels heavier than the other.

As every sensation is attended with an idea, and leaves behind it an idea in the mind which can be reproduced at will, we are enabled to compare the idea of a past sensation with another sensation really present. Thus we can compare the weight of one body with another which we had previously felt, of which the idea is retained in our mind. Weber was indeed able to distinguish in this manner between temperatures, experienced one after the other, better than between temperatures to which the two hands were simultaneously subjected. This power of comparing present with past sensations diminishes, however, in proportion to the time which has elapsed between them. *After-sensations* left by impressions on nerves of common sensibility or touch are very vivid and durable. As long as the condition into which the stimulus has thrown the organ endures, the sensation also remains, though the exciting cause should have long ceased to act. Both painful and pleasurable sensations afford many examples of this fact.

Subjective sensations, or sensations dependent on internal causes, are in no sense more frequent than in the sense of touch. All the sensations of pleasure and pain, of heat and cold, of lightness and weight, of fatigue, etc., may be produced by internal causes. Neuralgic pains, the sensation of rigor, formication or the creeping of ants, and the states of the sexual organs occurring during sleep, afford striking examples of subjective sensations. The mind has a remarkable power of exciting sensations in the nerves of common sensibility ; just as the thought of the nauseous excites sometimes the sensation of nausea, so the idea of pain gives rise to the actual sensation of pain in a part predisposed to it ; numerous examples of this influence might be quoted.

Taste.

Conditions necessary.—The conditions for the perceptions of taste are :—1, the presence of a nerve and nerve-centre with special endowments ; 2, the excitation of the nerve by the sapid matters, which for this purpose must be in a state of solution. The nerves concerned in the production of the sense of taste have been already considered (pp. 626 and 630). The mode of action of the substances which excite taste consists in the production of a hange in the condition of the gustatory nerves, and the conducion of the stimulus thus produced to the nerve-centre ; and, accordng to the difference of the substances, an infinite variety of changes f condition of the nerves, and consequently of stimulations of he gustatory centre, may be induced. The matters to be tasted nust either be in solution or be soluble in the moisture covering he tongue ; hence insoluble substances are usually tasteless, and roduce merely sensations of touch. Moreover, for the perfect ction of a sapid, as of an odorous substance, it is necessary that he sentient surface should be moist. Hence, when the tongue nd fauces are dry, sapid substances, even in solution, are with ifficulty tasted.

The nerves of taste, like the nerves of other special senses, may have their eculiar properties excited by various other kinds of irritation, such as lectricity and mechanical impressions. Thus, Henle observed that a small urrent of air directed upon the tongue gives rise to a cool saline taste, like hat of saltpetre ; and Baly has shown that a distinct sensation of taste, imilar to that caused by electricity, may be produced by a smart tap applied o the papillæ of the tongue. Moreover, the mechanical irritation of the auces and palate produces the sensation of nausea, which is probably only modification of taste.

Seat of sensation.—The principal seat of the sense of taste is he tongue. But the results of experiments as well as ordinary xperience show that the soft palate and its arches, the uvula, tonsils, and probably the upper part of the pharynx, are endowed with taste. These parts, together with the base and posterior parts of the tongue, are supplied with branches of the glossopharyngeal nerve, and evidence has been already adduced that the sense of taste is conferred upon them by this nerve. In most, though not in all persons, the anterior parts of the tongue, specially the edges and tip, are endowed with the sense of taste. The middle of the dorsum is only feebly endowed with this sense, probably because of the density and thickness of the epithelium overing the filiform papillæ of this part of the tongue, which will prevent the sapid substances from penetrating to their sensitive parts. The gustatory property of the anterior part of the tongue is due, as already said (p. 626), to the lingual or gustatory branch f the fifth nerve.

Structure of the Tongue.—The tongue is a muscular organ overed by mucous membrane. The muscles, which form the greater part of the substance of the tongue (*intrinsic* muscles) are termed *linguales;* and by these, which are attached to the mucous membrane chiefly, its smaller and more delicate movements are chiefly performed.

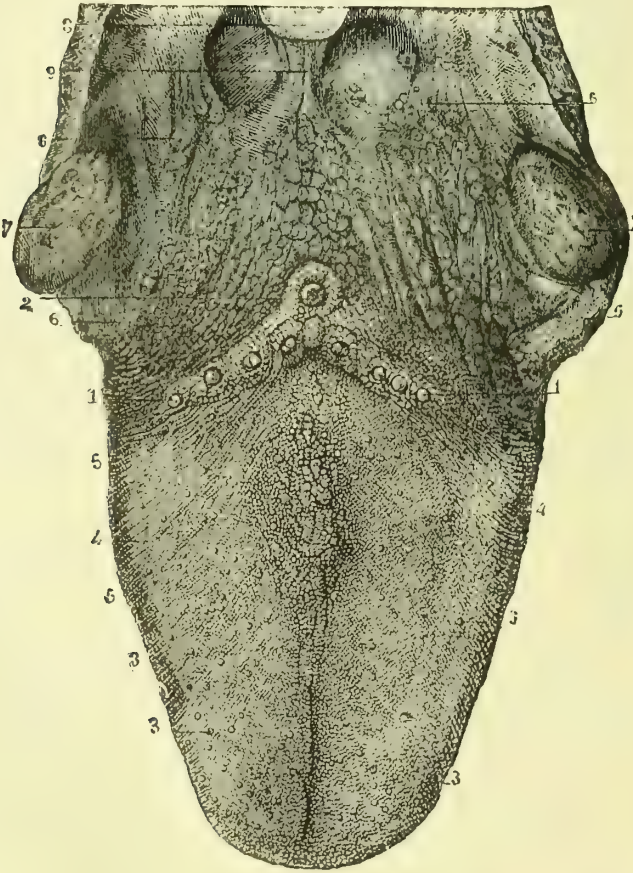


Fig. 349.—*Papillar surface of the tongue, with the fauces and tonsils.* 1, 1, circumvallate papillæ, in front of 2, the foramen cæcum; 3, fungiform papillæ; 4, filiform and conical papillæ; 5, transverse and oblique rugæ; 6, mucous glands at the base of the tongue and in the fauces; 7, tonsils; 8, part of the epiglottis; 9, median glosso-epiglottidean fold (frænum epiglottidis). (From Sappey.)

By other muscles (*extrinsic* muscles) as the genio-hyoglossus, the styloglossus, etc., the tongue is fixed to surrounding parts; and by this group of muscles its larger movements are performed.

The mucous membrane of the tongue resembles other mucous membranes (p. 397) in essential points of structure, but contains *papillæ*, more or less peculiar to itself; peculiar, however, in details of structure and arrangement, not in their nature. The tongue is beset with numerous mucous follicles and glands. The use of the tongue in relation to mastication and deglutition has already been considered (pp. 278 and 294).

The larger *papillæ* of the tongue are thickly set over the anterior two-thirds of its upper surface, or *dorsum* (fig. 349), and give to it its characteristic roughness. In carnivorous animals, especially those of the cat tribe, the papillæ attain a large size, and are developed into sharp recurved horny spines. Such papillæ cannot be regarded as sensitive, but they enable the tongue to play the part of a most efficient rasp, as in scraping bones, or of a comb in cleaning their fur. Their greater prominence than those of the skin is due to their interspaces not being filled up with epithelium, as the interspaces of the papillæ of the skin are. The papillæ of the tongue present several diversities of form; but three principal varieties, differing both in seat and general characters, may usually be distinguished, namely, the (1) *circumvallate*, the (2) *fungiform*, and the (3) *filiform* papillæ. Essentially these have all of them the same structure, that is to say, they are all formed by a projection of the mucous membrane, and contain special branches of blood-vessels and nerves. In details of structure, however, they differ considerably one from another.

The surface of each kind is studded by minute conical processes of mucous membrane, which thus form secondary papillæ.

Simple papillæ also occur over most other parts of the tongue not occupied by the compound papillæ, and extend for some distance behind the papillæ circumvallatæ. The mucous membrane immediately in front of the epiglottis is, however, free from them. They are commonly buried beneath the epithelium; hence they are often overlooked.

(1.) *Circumvallate.*—These papillæ (fig. 350), eight or ten in number, are situate in two V-shaped lines at the base of the tongue (1, 1, fig. 349). They are circular elevations from $\frac{1}{20}$th to $\frac{1}{12}$th of an inch wide, each with a central depression, and surrounded by a circular fissure, at the outside of which again is a slightly elevated ring, both the central elevation and the ring being formed of close set simple papillæ (fig. 350).

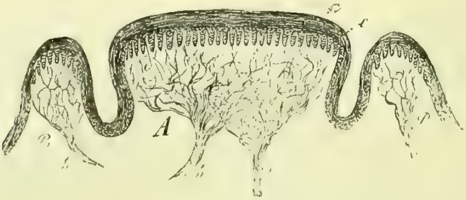


Fig. 350.—*Vertical section of a circumvallate papilla* $\frac{10}{1}$.—A, the papillæ; B, the surrounding wall; *a*, the epithelial covering; *b*, the nerves of the papilla and wall spreading towards the surface; *c*, the secondary papillæ. (Kölliker.)

(2.) *Fungiform.*—The fungiform papillæ (3, fig. 349) are scattered chiefly over the sides and tip, and sparingly over the middle of the dorsum, of the tongue; their name is derived from their being usually narrower at their base than at their summit. They also consist of groups of simple papillæ (A. fig. 351), each of which contains in its interior a loop of capillary blood-vessels (B.), and a nerve-fibre.

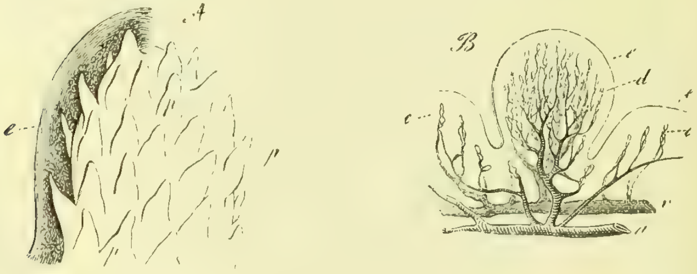


Fig. 351.—*Surface and section of the fungiform papillæ.* A, the surface of a fungiform papilla, partially denuded of its epithelium; *p*, secondary papillæ; *e*, epithelium. B, section of a fungiform papilla with the blood-vessels injected; *a*, artery; *v*, vein; *c*, capillary loops of similar papillæ in the neighbouring structure of the tongue; *d*, capillary loops of the secondary papillæ; *e*, epithelium. (From Kölliker, after Todd and Bowman.)

(3.) *Conical or Filiform.*—These, which are the most abundant papillæ, are scattered over the whole surface of the tongue, but especially over the middle of the dorsum (fig. 349). They vary in shape somewhat, but for the most part are conical or filiform, and covered by a thick layer of epidermis, which is arranged over them, either in an imbricated manner, or is prolonged from their surface in the form of fine stiff projections, hair-like in appearance, and in some instances in structure also (fig. 352). From their peculiar structure, it seems likely that these papillæ have a mechanical function, or one allied to that of touch rather than of taste; the latter sense being probably seated especially in the other two varieties of papillæ, the *circumvallate* and the *fungiform*.

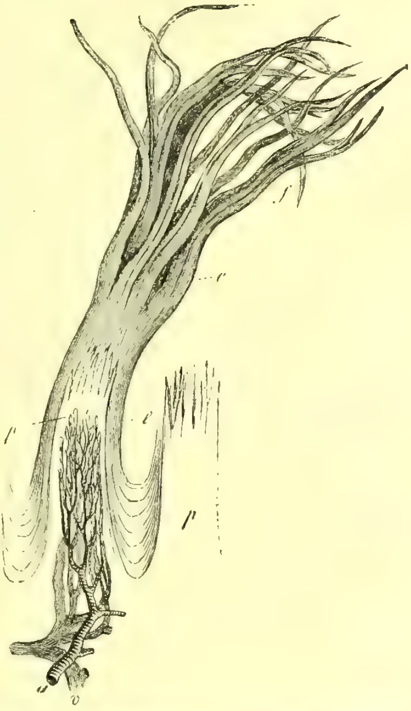


Fig. 352.—*Two filiform papillæ*, one with epithelium, the other without. $\frac{35}{1}$.—*p*, the substance of the papillæ dividing at their upper extremities into secondary papillæ; *a*, artery, and *v*, vein, dividing into capillary loops; *e*, epithelial covering, laminated between the papillæ, but extended into hair-like processes, *f*, from the extremities of the secondary papillæ. (From Kölliker, after Todd and Bowman.)

The *epithelium* of the tongue is stratified with the upper layers of the squamous kind. It covers every part of the surface; but over the fungiform papillæ forms a thinner layer than elsewhere. The epithelium covering the filiform papillæ is extremely dense and thick, and, as before mentioned, projects from their sides and summits in the form of long, stiff, hair-like processes (fig. 352). Many of these processes bear a close resemblance to hairs. Blood-vessels and nerves are supplied freely to the papillæ. The nerves in the fungiform and circumvallate papillæ form a kind of plexus, spreading out brush-wise (fig. 350), but the exact mode of termination of the nerve-filaments is not certainly known.

Taste goblets.—In the circumvallate papillæ of the tongue of man peculiar structures known as *gustatory buds* or *taste goblets*, have been discovered (Loven, Schwalbe). They are of an oval shape, and consist of a number of closely packed, very narrow and fusiform, cells (*gustatory cells*). This central core of gustatory cells is enclosed in a single layer of broader fusiform cells (*encasing cells*). The gustatory cells terminate in fine spikes not unlike cilia, which project on the free surface (fig. 353).

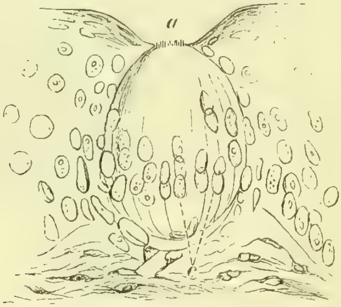


Fig. 353.—*Taste-goblet from dog's epiglottis* (laryngeal surface near the base), precisely similar in structure to those found in the tongue. *a*, depression in epithelium over goblet; below the letter are seen the fine hair-like processes in which the cells terminate; *c*, two nuclei of the axial (gustatory) cells. The more superficial nuclei belong to the superficial (encasing) cells; the converging lines indicate the fusiform shape of the encasing cells. × 400. (Schofield.)

These bodies also occur side by side in considerable numbers in the epithelium of the papilla foliata, which is situated near the root of the tongue in the rabbit, and also in man. Similar "taste-goblets" also occur pretty evenly distributed on the posterior (laryngeal) surface of the epiglottis (Verson, Schofield). It seems probable, from their distribution, that all these so-called taste-goblets are gustatory in function, though no nerves have been distinctly traced into them.

Other Functions of the Tongue.—Besides the sense of taste, the tongue, by means also of its papillæ, is endued, (2) especially at its sides and tip, with a very delicate and accurate sense of touch (p. 653), which renders it sensible of the impressions of heat and cold, pain and mechanical pressure, and consequently of the form of surfaces. The tongue may lose its common sensibility, and still retain the sense of taste, and *vice versâ.* This fact renders it probable that, although the senses of taste and of touch may be exercised by the same papillæ supplied by the same nerves, yet the nervous conductors for these two different sensations are distinct, just as the nerves for smell and common sensibility in the nostrils are distinct; and it is quite conceivable that the same nervous trunk may contain fibres differing essentially in their specific properties. Facts already detailed (p. 626) seem to prove that the lingual branch of the fifth nerve is the conductor of sensations of taste in the anterior part of the tongue; and it is also certain, from the marked manifestations of pain to which its division in animals gives rise, that it is likewise a nerve of common sensibility. The glosso-pharyngeal also seems to contain fibres both of common sensation and of the special sense of taste.

The functions of the tongue in connection with (3) speech, (4) mastication, (5) deglutition, (6) suction, have been referred to in other chapters.

Taste and Smell; Perceptions.—The concurrence of common and special sensibility in the same part makes it sometimes difficult to determine whether the impression produced by a substance is perceived through the ordinary sensitive fibres, or through those of the sense of taste. In many cases, indeed, it is probable that both sets of nerve-fibres are concerned, as when irritating acrid substances are introduced into the mouth.

Much of the perfection of the sense of taste is often due to the sapid substances being also odorous, and exciting the simultaneous action of the sense of smell. This is shown by the imperfection of the taste of such substances when their action on the olfactory nerves is prevented by closing the nostrils. Many fine wines lose much of their apparent excellence if the nostrils are held close while they are drunk.

Varieties of Tastes.—Among the most clearly defined tastes are the sweet and bitter (which are more or less opposed to each other), the acid, alkaline, and saline tastes. Acid and alkaline taste may be excited by electricity. If a piece of zinc be placed beneath and a piece of copper above the tongue, and their ends brought into contact, an acid taste (due to the feeble galvanic current) is produced. The delicacy of the sense of taste is sufficient to discern 1 part of sulphuric acid in 1000 of water; but it is far surpassed in acuteness by the sense of smell.

After-tastes.—Very distinct sensations of taste are frequently left after the substances which excited them have ceased to act on the nerve; and such sensations often endure for a long time, and modify the taste of other substances applied to the tongue afterwards. Thus, the taste of sweet substances spoils the flavour of wine, the taste of cheese improves it. There appears, therefore, to exist the same relation between tastes as between colours, of which those that are opposed or complementary render each other more vivid, though no general principles governing this relation have been discovered in the case of tastes. In the art of cooking, however, attention has at all times been paid to the consonance or harmony of flavours in their combination or order of succession, just as in painting and music the fundamental principles of harmony have been employed empirically while the theoretical laws were unknown.

Frequent and continued repetitions of the same taste render the perception of it less and less distinct, in the same way that a colour becomes more and more dull and indistinct the longer the eye is fixed upon it. Thus, after frequently tasting first one and then the other of two kinds of wine, it becomes impossible to discriminate between them.

The simple contact of a sapid substance with the surface of the gustatory organ seldom gives rise to a distinct sensation of taste; it needs to be diffused over the surface, and brought into intimate contact with the sensitive parts by compression, friction, and motion between the tongue and palate.

Subjective Sensations of Taste.—The sense of taste seems capable of being excited only by external causes, such as changes in the conditions of the nerves or nerve-centres, produced by congestion or other causes, which excite subjective sensations in the other organs of sense. But little is known of the subjective sensations of taste; for it is difficult to distinguish the phenomena from the effects of external causes, such as changes in the nature of the secretions of the mouth.

Smell.

Conditions necessary.—(1.) The first conditions essential to the sense of smell are a special *nerve* and *nerve-centre*, the changes in whose condition are perceived in sensations of odour;

for no other nervous structure is capable of these sensations, even though acted on by the same causes. The same substance which excites the sensation of smell in the olfactory centre may cause another peculiar sensation through the nerves of taste, and may produce an irritating and burning sensation on the nerves of touch ; but the sensation of odour is yet separate and distinct from these, though it may be simultaneously perceived. (2.) The second condition of smell is a peculiar change produced in the olfactory nerve and its centre by the stimulus or odorous substance. (3.) The material causes of odours are, usually, in the case of animals living in the air, either solids suspended in a state of extremely fine division in the atmosphere ; or gaseous exhalations often of so subtile a nature that they can be detected by no other re-agent than the sense of smell itself. The matters of odour must, in all cases, be dissolved in the mucus of the mucous membrane before they can be immediately applied to, or affect the olfactory nerves ; therefore a further condition necessary for the perception of odours is, that the mucous membrane of the nasal cavity be moist. When the Schneiderian membrane is dry, the sense of smell is impaired or lost ; in the first stage of catarrh, when the secretion of mucus within the nostrils is lessened, the faculty of perceiving odour is either lost, or rendered very imperfect. (4.) In animals living in the air, it is also requisite that the odorous matter should be transmitted in a current through the nostrils. This is effected by an inspiratory movement, the mouth being closed ; hence we have voluntary influence over the sense of smell ; for by interrupting respiration we prevent the perception of odours, and by repeated quick inspiration, assisted, as in the act of *sniffing*, by the action of the nostrils, we render the impression more intense (see p. 248). An odorous substance in a liquid form injected into the nostrils appears incapable of giving rise to the sensation of smell : thus Weber could not smell the slightest odour when his nostrils were completely filled with water containing a large quantity of eau de Cologne.

Seat of the Sense of Smell.—The human organ of smell is formed by the filaments of the olfactory nerves, distributed in the mucous membrane covering the upper third of the septum of the nose, the superior turbinated or spongy bone, the upper part of the middle turbinated bone, and the upper wall of the nasal cavities beneath the cribriform plates of the ethmoid bones (figs. 354 and 355). The olfactory region is covered by cells of *cylindrical* epithelium, prolonged at their deep extremities into fine branched processes, but not ciliated; and interspersed with these are fusiform (*olfactory*) cells, with both superficial and deep processes (fig. 356), the latter being probably connected with the terminal filaments of the olfactory nerve. The lower, or respiratory part, as it is called, of the nasal fossæ is lined by *cylindrical ciliated* epithelium, except in the region of the nostrils, where it is *squamous*. The branches of the olfactory nerves retain much of the same soft and greyish texture which distinguishes those of the olfactory *tracts* within the cranium. Their filaments, also, are peculiar, more resembling those of the sympathetic nerve than the filaments of the other cerebral nerves do, containing no outer white substance, and being finely granular and nucleated. The sense of smell is derived exclusively through those parts of the nasal cavities in which the olfactory nerves are distributed; the accessory cavities or sinuses communicating with the nostrils seem to have no relation to it. Air impregnated with the vapour of camphor was injected into the frontal sinus through a fistulous opening, and odorous substances have been injected into the antrum of Highmore; but in neither case was any odour perceived by the

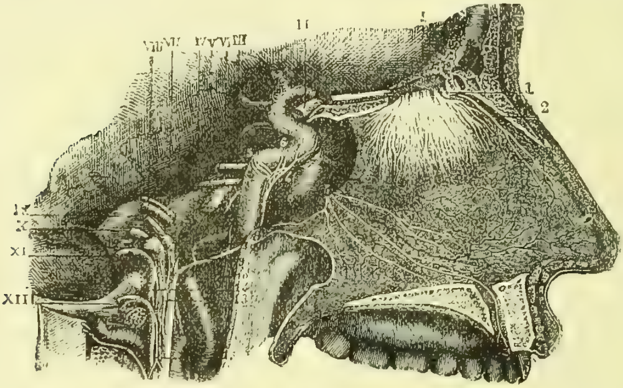


Fig. 354.—*Nerves of the septum nasi*, seen from the right side. $\frac{2}{3}$.—I, the olfactory bulb; 1, the olfactory nerves passing through the foramina of the cribriform plate, and descending to be distributed on the septum; 2, the internal or septal twig of the nasal branch of the ophthalmic nerve; 3, naso-palatine nerves. (From Sappey, after Hirschfeld and Leveillé.)

patient. The purposes of these sinuses appear to be, that the bones, necessarily large for the action of the muscles and other parts connected with them, may be as light as possible, and that there may be more room for the resonance of the air in vocalising. The former purpose, which is in other bones obtained by filling their cavities with fat, is here attained, as it is in many bones of birds, by their being filled with air.

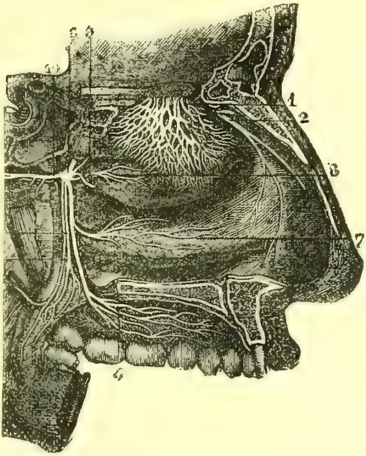


Fig. 355.—*Nerves of the outer walls of the nasal fossæ.* $\frac{3}{5}$.—1, network of the branches of the olfactory nerve, descending upon the region of the superior and middle turbinated bones; 2, external twig of the ethmoidal branch of the nasal nerves; 3, spheno-palatine ganglion; 4, ramification of the anterior palatine nerves; 5, posterior, and 6, middle divisions of the palatine nerves; 7, branch to the region of the inferior turbinated bone; 8, branch to the region of the superior and middle turbinated bones; 9, naso-palatine branch to the septum cut short. (From Sappey, after Hirschfeld and Leveillé.)

Other Functions of the Olfactory Region. — All parts of the nasal cavities, whether or not they can be the seats of the sense of smell, are endowed with common sensibility by the nasal branches of the first and second divisions of the fifth nerve. Hence the sensations of cold, heat, itching, tickling, and pain; and the sensation of tension or pressure in the nostrils. That these nerves cannot perform the function of the olfactory nerves is proved by cases in which the sense of smell is lost, while the mucous membrane of the nose remains susceptible of the various modifications of common sensation or touch. But it is often difficult to distinguish the sensation of smell from that of mere feeling, and to ascertain what belongs to each separately. This is the case particularly with the sensations excited in the nose by acrid vapours, as of ammonia, horse-radish, mustard, etc., which resemble much the sensations of the nerves of touch; and the difficulty is the greater, when it is remembered that these acrid vapours have nearly the same action upon the mucous membrane of the eyelids. It was because the common sensibility of the nose to these irritating substances remained after the destruction of the olfactory nerves, that Magendie was led to the erroneous belief that the fifth nerve might exercise this special sense.

Varieties of Odorous Sensations.—Animals do not all equally perceive the same odours; the odours most plainly perceived by an herbivorous animal and by a carnivorous animal are different. The Carnivora have the power of detecting most accurately by the smell the special peculiarities of animal matters, and of tracking other animals by the scent; but have apparently very little sensibility to the odours of plants and flowers. Herbivorous animals are peculiarly sensitive to the latter, and have a narrower sensibility to animal odours, especially to such as proceed from other individuals than their own species. Man is far inferior to many animals of both classes in respect of the acuteness of smell; but his sphere of susceptibility to various odours is more uniform and extended. The cause of this difference lies probably in the endowments of the cerebral parts of the olfactory apparatus. The delicacy of the sense of smell is most remarkable; it can discern the presence of bodies in quantities so minute as to be undiscoverable even by spectrum analysis; $\frac{3}{100,000,000}$ of a grain of musk can be distinctly smelt (Valentin). Opposed to the sensation of an agreeable odour is that of a disagreeable or disgusting odour, which corresponds to the sensations of pain, dazzling and disharmony of colours, and dissonance in the other senses. The cause of this difference in the effect of different odours is unknown: but this much is certain, that odours are pleasant or offensive in a relative sense only, for many animals pass their existence in the midst of odours which to us are highly disagreeable. A great difference in this respect is, indeed, observed amongst men: many odours, generally thought agreeable, are to some persons intolerable; and different persons describe differently the sensations that they severally derive from the same odorous substances. There seems also to be in some persons an insensibility to certain odours, com-

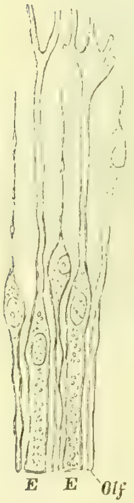


Fig. 356.—*Epithelial and olfactory cells of man.* The letters are placed on the free surface. *E, E,* epithelial cells; *Olf.*, olfactory cells. (Max Schultze.)

parable with that of the eye to certain colours; and among different persons, as great a difference in the acuteness of the sense of smell as among others in the acuteness of sight. We have no exact proof that a relation of harmony and disharmony exists between odours as between colours and sounds; though it is probable that such is the case, since it certainly is so with regard to the sense of taste; and since such a relation would account in some measure for the different degrees of perceptive power in different persons; for as some have no ear for music (as it is said), so others have no clear appreciation of the relation of odours, and therefore little pleasure in them.

Subjective Sensations of Smell.—The sensations of the olfactory nerves, independent of the external application of odorous substances, have hitherto been little studied. The friction of the electric machine produces a smell like that of phosphorus. Ritter, too, has observed, that when galvanism is applied to the organ of smell, besides the impulse to sneeze, and the tickling sensation excited in the filaments of the fifth nerve, a smell like that of ammonia was excited by the negative pole, and an acid odour by the positive pole; whichever of these sensations were produced, it remained constant as long as the circle was closed, and changed to the other at the moment of the circle being opened. *Subjective* sensations occur frequently in connection with the sense of smell. Frequently a person smells something which is not present, and which other persons cannot smell; this is very frequent with nervous people, but it occasionally happens to every one. In a man who was constantly conscious of a bad odour, the arachnoid was found after death to be beset with deposits of bone; and in the middle of the cerebral hemispheres were scrofulous cysts in a state of suppuration. Dubois was acquainted with a man who, ever after a fall from his horse, which occurred several years before his death, believed that he smelt a bad odour.

Hearing.

Anatomy of the Ear.—For descriptive purposes, the Ear, or Organ of Hearing, is divided into three parts, (1) the *external*, (2) the *middle*, and (3) the *internal* ear. The two first are only accessory to the third or internal ear, which contains the essential parts of an organ of hearing. The accompanying figure shows very well the relation of these divisions,—one to the other (fig. 357).

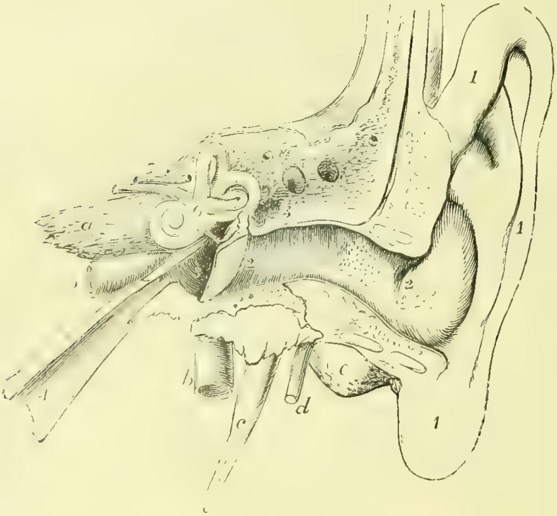


Fig. 357. *Diagrammatic view from before of the parts composing the organ of hearing of the left side.* The temporal bone of the left side, with the accompanying soft parts, has been detached from the head, and a section has been carried through it transversely, so as to remove the front of the meatus externus, half the tympanic membrane, the upper and anterior wall of the tympanum and Eustachian tube. The meatus internus has also been opened, and the bony labyrinth exposed by the removal of the surrounding parts of the petrous bone. 1, the pinna and lobe; 2, 2', meatus externus; 2', membrana tympani; 3, cavity of the tympanum; 3', its opening backwards into the mastoid cells; between 3 and 3', the chain of small bones; 4, Eustachian tube; 5, meatus internus, containing the facial (uppermost) and the auditory nerves; 6, placed on the vestibule of the labyrinth above the fenestra ovalis; *a*, apex of the petrous bone; *b*, internal carotid artery; *c*, styloid process; *d*, facial nerve issuing from the stylomastoid foramen; *e*, mastoid process; *f*, squamous part of the bone covered by integument, &c. (Arnold.)

(1.) *External Ear.*—The external ear consists of the *pinna* or *auricle*, and the external *auditory canal* or *meatus.*

The principal parts of the *pinna* (fig. 358 A) are two prominent rims enclosed one within the other (*helix* and *antihelix*), and enclosing a central hollow named the *concha;* in front of the concha, a prominence directed backwards, the *tragus*, and opposite to this, one directed forwards, the *antitragus.* From the concha, the auditory canal, with a slight arch directed upwards, passes inwards and a little forwards to the membrana tympani, to which it thus serves to convey the vibrating air. Its outer part consists of fibro-cartilage continued from the concha; its inner part of bone. Both are lined by skin continuous with that of the pinna, and extending over the outer part of the *membrana tympani.*

Towards the outer part of the canal are fine hairs and sebaceous glands, while deeper in the canal are small glands, resembling the sweat-glands in structure which secrete a peculiar yellow substance called *cerumen*, or ear-wax.

(2.) *Middle Ear* or *Tympanum*.—The *middle* ear, or *tympanum* (3, fig. 357), is separated by the *membrana tympani* from the external auditory canal. It is a cavity in the temporal bone, opening through its anterior and inner wall into the Eustachian tube, a cylindriform flattened canal, dilated at both ends, composed partly of bone and partly of cartilage, and lined with mucous membrane, which forms a communication between the tympanum and the pharynx. It opens into the cavity of the pharynx just behind the posterior aperture of the nostrils. The cavity of the tympanum communicates posteriorly with air-cavities, the *mastoid cells* in the mastoid process of the temporal bone; but its only opening to the external air is through the Eustachian tube (4, fig. 357). The walls of the tympanum are osseous, except where apertures in them are closed with membrane, as at the fenestra rotunda, and fenestra ovalis, and at the outer part where the bone is replaced by the *membrana tympani*. The cavity of the tympanum is lined with mucous membrane, the epithelium of which is ciliated and continuous with that of the pharynx. It contains a chain of small bones (*ossicula auditus*) which extends from the membrana tympani to the fenestra ovalis.

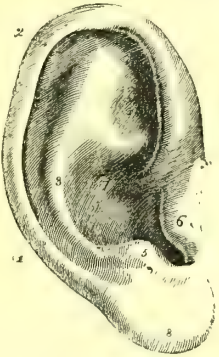


Fig. 358.—*Outer surface of the pinna of the right auricle.* 1, helix; 2, fossa of the helix; 3, antihelix; 4, fossa of the antihelix; 5, antitragus; 6, tragus; 7, concha; 8, lobule. $\frac{2}{3}$.

The *membrana tympani* is placed in a slanting direction at the bottom of the external auditory canal, its plane being at an angle of about 45° with the lower wall of the canal. It is formed chiefly of a tough and tense fibrous membrane, the edges of which are set in a bony groove: its outer surface is covered with a continuation of the cutaneous lining of the auditory canal, its inner surface with part of the ciliated mucous membrane of the tympanum.

The small bones or *ossicles* of the ear are three; named *malleus*, *incus*, and *stapes*. The *malleus*, or hammer-bone, is attached by a long slightly-curved process, called its handle, to the membrana tympani; the line of attachment being vertical, including the whole length of the handle, and extending from the upper border to the centre of the membrane. The head of the malleus is irregularly rounded; its neck, or the line of boundary between it and the handle, supports two processes; a *short* conical one, which receives the insertion of the *tensor tympani*, and a *slender* one, *processus gracilis*, which extends forwards, and to which the *laxator tympani* muscle is attached. The *incus*, or anvil-bone, shaped like a bicuspid molar tooth, is articulated by its broader part, corresponding with the surface of the crown of a tooth, to the malleus. Of its two fang-like processes, one, directed backwards, has a free end lodged in a depression in the mastoid bone; the other, curved downwards and more pointed, articulates by means of a roundish tubercle, formerly called *os orbiculare*, with the stapes, a little bone shaped exactly like a stirrup, of which the base or bar fits into the fenestra ovalis. To the neck of the stapes, a short process, corresponding with the loop of the stirrup, is attached the *stapedius* muscle.

The Ossicula.—The bones of the ear are covered with mucous membrane reflected over them from the wall of the tympanum; and are movable both altogether and one upon the other. The malleus moves and vibrates with every movement and vibration of the membrana tympani, and its movements are communicated through the incus to the stapes, and through it to the membrane closing the fenestra ovalis. The malleus, also, is movable in its articulation with the incus; and the membrana tympani moving with it is altered in its degree of tension by the laxator and tensor tympani muscles. The stapes is movable on the process of the incus, when the stapedius muscle acting, draws it backwards. The axis round which the malleus and incus rotate is the line joining the processus gracilis of the malleus and the posterior (short) process of the incus.

(3.) *Internal Ear.*—The proper organ of hearing is formed by the distribution of the auditory nerve within the *internal ear*, or *labyrinth* of the ear, a set of cavities within the petrous portion of the temporal bone. The bone which forms the walls of these cavities is denser than that around it, and forms the *osseous labyrinth;* the membrane within the cavities forms the *membranous labyrinth.* The membranous labyrinth contains a fluid called *endolymph;* while outside it, between it and the osseous labyrinth, is a fluid called *perilymph.*

The osseous labyrinth consists of three principal parts, namely, the *vestibule*, the *cochlea*, and the *semicircular canals.*

The vestibule is the middle cavity of the labyrinth, and the central organ of the whole auditory apparatus. It presents, in its inner wall, several openings for the entrance of the divisions of the auditory nerve; in its outer wall, the *fenestra ovalis* (2, fig. 359), an opening filled by the base of the *stapes*, one of the small bones of the ear; in its posterior and superior walls, five openings by which the *semicircular canals* communicate with it: in its anterior wall, an opening leading into the *cochlea*. The hinder part of the inner wall, of the vestibule also presents an opening, the orifice of the *aquæductus vestibuli*, a canal leading to the posterior margin of the petrous bone, with uncertain contents and unknown purpose.

The *semicircular canals* (figs. 359, 360), are three arched cylindriform bony canals, set in the substance of the petrous bone. They all open at both ends into the vestibule (two of them first coalescing). The ends of each are dilated just before opening into the vestibule; and one end of each being more dilated than the other is called an *ampulla*. Two of the canals form nearly vertical arches; of these the superior is also anterior; the posterior is inferior; the third canal is horizontal, and lower and shorter than the others.

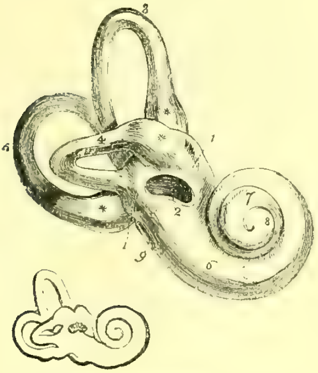


Fig. 359.—*Right bony labyrinth*, viewed from the outer side. The specimen here represented is prepared by separating piecemeal the looser substance of the petrous bone from the dense walls which immediately enclose the labyrinth. 1, the vestibule; 2, fenestra ovalis; 3, superior semicircular canal; 4, horizontal or external canal; 5, posterior canal; *, ampullæ of the semicircular canals; 6, first turn of the cochlea; 7, second turn; 8, apex; 9, fenestra rotunda. The smaller figure in outline below shows the natural size. $\frac{2\frac{1}{2}}{1}$. (Sömmering.)

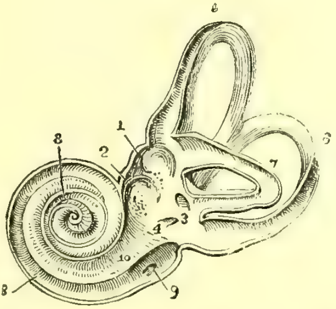


Fig. 360.—*View of the interior of the left labyrinth*. The bony wall of the labyrinth is removed superiorly and externally. 1, fovea hemielliptica; 2, fovea hemispherica; 3, common opening of the superior and posterior semicircular canals; 4, opening of the aqueduct of the vestibule; 5, the superior, 6, the posterior, and 7, the external semicircular canals; 8, spiral tube of the cochlea (scala tympani); 9, opening of the aqueduct of the cochlea; 10, placed on the lamina spiralis in the scala vestibuli. $\frac{2\frac{1}{2}}{1}$ (Sömmering.)

The *cochlea* (6, 7, 8, figs. 359 and 360), a small organ, shaped like a common snail-shell, is seated in front of the vestibule, its base resting on the bottom of the internal meatus, where some apertures transmit to it the cochlear filaments of the auditory nerve. In its axis, the cochlea is traversed by a conical column, the *modiolus*, around which a *spiral canal* winds with about two turns and a half from the base to the apex. At the apex of the cochlea the canal is closed; at the base it presents three openings, of which one, already mentioned, communicates with the vestibule; another called *fenestra rotunda*, is separated by a membrane from the cavity of the tympanum; the third is the orifice of the *aquæductus cochleæ*, a canal leading to the jugular fossa of the petrous bone, and corresponding, at least in obscurity of purpose and origin, to the aquæductus vestibuli. The spiral canal is divided into two passages, or scalæ, by a partition of bone and membrane, the *lamina spiralis.* The osseous part or *zone* of this lamina is connected with the modiolus; the membranous part, with a muscular zone, according to Todd and Bowman, forming its outer margin, is attached to the outer wall of the canal. Commencing at the base of the cochlea, between its vestibular and tympanic openings, they form a partition between these apertures; the two scalæ are, therefore, in correspondence with this arrangement, named *scala vestibuli* and *scala tympani* (fig. 361). At the apex of the cochlea, the lamina spiralis ends in a small *hamulus*, the inner and concave part of which, being detached from the summit of the modiolus, leaves a small aperture named *helicotrema*, by which the two scalæ, separated in all the rest of their length, communicate.

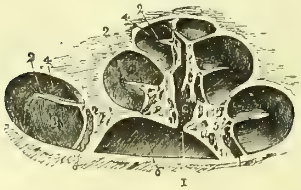


Fig. 361.—*View of the osseous cochlea divided through the middle.* 1, central canal of the modiolus; 2, lamina spiralis ossea; 3, scala tympani; 4, scala vestibuli; 5, porous substance of the modiolus near one of the sections of the canalis spiralis modioli. $\frac{4}{1}$. (Arnold.)

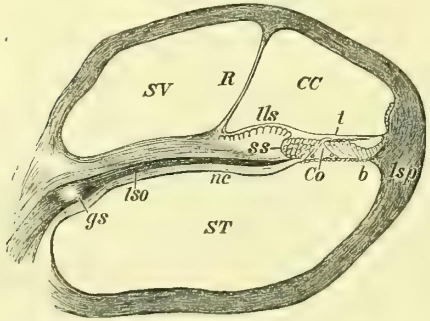


Fig. 362.—*Section through one of the coils of the cochlea* (diagrammatic). *S T*, scala tympani; *S V*, scala vestibuli; *C C*, canalis cochleæ or canalis membranaceus; *R*, membrane of Reissner; *l s o*, lamina spiralis ossea; *l l s*, limbus laminæ spiralis; *s s*, sulcus spiralis; *n c*, cochlear nerve; *g s*, ganglion spirale; *t*, membrana tectoria; (below the membrana tectoria is the lamina reticularis;) *b*, membrana basilaris; *Co*, rods of Corti; *l sp*, ligamentum spirale. (From *Quain's Anatomy.*)

Besides the "scala vestibuli" and "scala tympani," there is a third space between them, called *scala media* or *canalis membranaceus* (CC. fig. 362). In section it is triangular, its external wall being formed by the wall of the cochlea, its upper wall (separating it from the scala vestibuli) by the membrane of Reissner, and its lower wall (separating it from the scala tympani) by the basilar membrane, these two meeting at the outer edge of the bony lamina spiralis. Following the turns of the cochlea to its apex, the scala media there terminates blindly; while towards the base of the cochlea it is also closed with the exception of a very narrow passage (canalis reuniens) uniting it with the sacculus. The scala media (like the rest of the membranous labyrinth) contains "endolymph."

Organ of Corti.—Upon the basilar membrane are arranged cells of various shapes.

About midway between the outer edge of the lamina spiralis and the outer wall of the cochlea are situated the *rods of Corti*. Viewed sideways, the rods of Corti are seen to consist of an external and internal pillar, each rising from an expanded foot or *base* on the basilar membrane. They slant inwards towards each other, and each ends in a swelling termed the head; the head of the inner pillar overlying that of the outer (fig. 363). Each pair of pillars forms, as it were, a pointed roof arching over a space, and by a succession of them, a little tunnel is formed.

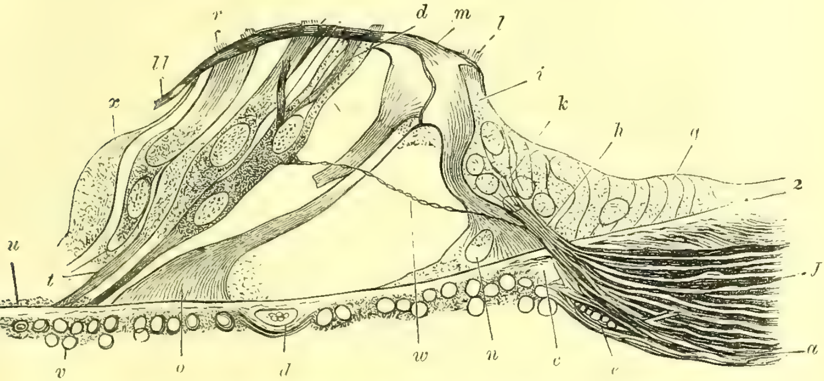


Fig. 363.—*Vertical section of the organ of Corti* from the dog. 1 to 2, homogeneous layer of the so-called membrana basilaris; *u*, vestibular layer; *v*, tympanal layer, with nuclei and protoplasm; *a*, prolongation of tympanal periosteum of lamina spiralis ossea; *c*, thickened commencement of the membrana basilaris near the point of perforation of the nerves *h*; *d*, blood-vessel (vas spirale); *e*, blood-vessel; *f*, nerves; *g*, the epithelium of the sulcus spiralis internus; *i*, internal or tufted cell, with basil process *k*, surrounded with nuclei and protoplasm (of the granular layer), into which the nerve-fibres radiate; *l*, hairs of the internal hair-cell; *n*, base or foot of inner pillar of organ of Corti; *m*, head of the same uniting with the corresponding part of an external pillar, whose under half is missing, while the next pillar beyond, *o*, presents both middle portion and base; *r*, *s*, *d*, three external hair cells; *t*, bases of two neighbouring hair or tufted cells; *x*, so-called supporting cell of Hensen; *w*, nerve-fibre terminating in the first of the external hair-cells; *l l* to *l*, lamina reticularis. × 800. (Waldeyer.)

It has been estimated that there are about 3000 of these pairs of pillars, in proceeding from the base of the cochlea towards its apex. They are found progressively to increase in length, and become more oblique; in other words, the tunnel becomes wider, but diminishes in height as we approach the apex of the cochlea. Leaning, as it were, against these external and internal pillars are certain other cells, of which the external ones terminate in small hair-like processes. Most of the above details are shown in the accompanying figure (fig. 363). This complicated structure rests, as we have seen, upon the basilar membrane; it is roofed in by a remarkable fenestrated membrane (lamina reticularis of Kölliker) into the fenestræ of which the tops of the various rods and cells are received. When viewed from above, the organ of Corti shows a remarkable resemblance to the key-board of a piano. In close relation with the rods of Corti and the cells inside and outside them, and probably projecting by free ends into the little "tunnel" containing fluid (roofed in by them), are filaments of the auditory nerve.

Membranous Labyrinth.—This corresponds generally with the form of the osseous labyrinth, so far as regards the vestibule and semicircular canals, but is separated from the walls of these parts by fluid, except where the nerves enter into connection within it. As already mentioned, the membranous labyrinth contains a fluid called *endolyph;* and between its outer surface and the inner surface of the walls of the vestibule and semicircular canals is another collection of similar fluid, called *perilymph;* so that all the sonorous vibrations impressing the auditory nerves on these parts of the internal ear, are conducted through fluid to a membrane suspended in and containing fluid. In the cochlea, the membranous labyrinth completes the septum between the two *scalæ* and encloses a spiral canal, previously mentioned, called *canalis membranaceus* or *canalis cochleæ* (fig. 362). The fluid in the *scalæ* of the cochlea is continuous with the perilymph in the vestibule and semicircular canals, and there is no fluid external to its lining membrane. The vestibular portion of the membranous labyrinth comprises two, probably communicating cavities, of which the larger and upper is named the *utriculus;* the lower, the *sacculus.* They are lodged in depressions in the bony labyrinth termed respectively "fovea hemielliptica" and "fovea hemispherica." Into the former open the orifices of the membranous semicircular canals; into the latter the *canalis cochleæ.* The membranous labyrinth of all these parts is laminated, transparent, very vascular, and covered on the inner surface with nucleated cells, of which those that line the ampullæ are prolonged into stiff hair-like processes; the same appearance, but to a much less degree, being visible in the *utricule* and *saccule.* In the cavities of the utriculus and sacculus are small masses of calcareous particles, *otoconia* or *otoliths;* and the same, although in more minute quantities, are to be found in the interior of some other parts of the membranous labyrinth.

Auditory Nerve.—For the appropriate exposure of the filaments of the auditory nerve to sonorous vibrations all the organs now described are provided. It is characterised as a nerve of special sense by its softness (whence it derived its name of *portio mollis* of the seventh pair), and by the fineness of its component fibres. It enters the labyrinth of the ear in two divisions; one for the vestibule and semicircular canals, and the other for the cochlea.

The branches for the vestibule spread out and radiate on the inner surface of the membranous labyrinth: their exact termination is unknown. Those for the semicircular canals pass into the ampullæ, and form, within each of them, a forked projection which corresponds with a septum in the interior of the ampulla. The branches for the cochlea enter it through orifices at the base of the modiolus, which they ascend, and thence successively pass into canals in the osseous part of the lamina spiralis. In the canals of this osseous part or zone, the nerves are arranged in a plexus, containing ganglion cells. Their ultimate termination is not known with certainty; but some of them, without doubt, end in the organ of Corti, probably in cells.

Physiology of Hearing.

All the acoustic contrivances of the organ of hearing are means for conducting the sound, just as the optical apparatus of the eye are media for conducting the light. Since all matter is capable of propagating sonorous vibrations, the simplest conditions must be sufficient for mere hearing; for all substances surrounding the auditory nerve would communicate sound to it. The whole development of the organ of hearing, therefore, can have for its object merely the *rendering more perfect* the propagation of the sonorous vibrations, and their *multiplication* by resonance; and, in fact, all the acoustic apparatus of the organ may be shown to have reference to these two principles.

Functions of the External Ear.—The external auditory passage influences the propagation of sound to the tympanum in three ways:—1, by causing the sonorous undulations, entering directly from the atmosphere, to be transmitted by the air in the passage immediately to the membrana tympani, and thus preventing them from being dispersed; 2, by the walls of the passage conducting the sonorous undulations imparted to the external ear itself, by the shortest path to the attachment of the membrana tympani, and so to this membrane; 3, by the resonance of the column of air contained within the passage; 4, the external ear, especially when the tragus is provided with hairs, is also, doubtless, of service in protecting the meatus and membrana tympani against dust, insects, and the like.

1. As a conductor of undulations of air, the external auditory passage receives the direct undulations of the atmosphere, of which those that enter in the direction of its axis produce the strongest impressions. The undulations which enter the passage obliquely are reflected by its parietes, and thus by reflexion reach the membrana tympani.

2. The walls of the meatus are also solid conductors of sound; for those vibrations which are communicated to the cartilage of the external ear, and not reflected from it, are propagated by the shortest path through the parietes of the passage to the membrana tympani. Hence, both ears being close stopped, the sound of a pipe is heard more distinctly when its lower extremity, covered with a membrane, is applied to the cartilage of the external ear itself, than when it is placed in contact with the surface of the head.

3. The external auditory passage is important, inasmuch as the air which it contains, like all insulated masses of air, increases the intensity of sounds by resonance.

Regarding the cartilage of the external ear, therefore, as a conductor of sonorous vibrations, all its inequalities, elevations, and depressions, which are useless with regard to reflexion, become of evident importance; for those elevations and depressions upon which the undulations fall perpendicularly, will be affected by them in the most intense degree; and, in consequence of the various forms and positions of these inequalities, sonorous undulations, in whatever direction they may come, must fall perpendicularly upon the tangent of some one of them. This affords an explanation of the extraordinary form given to this part.

Functions of the Middle Ear.—In animals living in the atmosphere, the sonorous vibrations are conveyed to the auditory nerve by three different media in succession; namely, the air, the solid parts of the body of the animal and of the auditory apparatus, and the fluid of the labyrinth. Sonorous vibrations are imparted too imperfectly from air to solid bodies, for the propagation of sound to the internal ear to be adequately effected by that means alone; yet already an instance of its being thus propagated has been mentioned. In passing from air directly into water, sonorous vibrations suffer also a considerable diminution of their strength; but if a tense membrane exists between the air and the water, the sonorous vibrations are communicated from the former to the latter medium with very great intensity. This fact, of which Müller gives experimental proof, furnishes at once an explanation of the use of the fenestra rotunda, and of the membrane closing it. They are the means of communicating, in full intensity, the vibrations of the air in the tympanum to the fluid of the labyrinth. This peculiar property of membranes is the result, not of their tenuity alone, but of the elasticity and capability of displacement of their particles ; and it is not impaired when, like the membrane of the fenestra rotunda, they are not impregnated with moisture.

Sonorous vibrations are also communicated without any perceptible loss of intensity from the air to the water, when to the membrane forming the medium of communication, there is attached a short, solid body, which occupies the greater part of its surface, and is alone in contact with the water. This fact elucidates the action of the fenestra ovalis, and of the plate of the stapes which occupies it, and, with the preceding fact, shows that both fenestræ—that closed by membrane only, and that with which the movable stapes is connected—transmit very freely the sonorous vibrations from the air to the fluid of the labyrinth.

A small, solid body, fixed in an opening by means of a border of membrane, so as to be movable, communicates sonorous vibrations from air on the one side, to water, or the fluid of the labyrinth, on the other side, much better than solid media not so constructed. But the propagation of sound to the fluid is rendered much more perfect if the solid conductor thus occupying the opening, or fenestra ovalis, is by its other end fixed to the middle of a tense membrane, which has atmospheric air on both sides. A tense membrane is a much better conductor of the vibrations of air than any other solid body bounded by definite surfaces : and the vibrations are also communicated very readily by tense membranes to solid bodies in contact with them. Thus, then, the *membrana tympani* serves for the transmission of sound from the air to the chain of auditory bones. Stretched tightly in its osseous ring, it vibrates with the air in the auditory passage, as any thin tense membrane will, when the air near it is thrown into vibrations by the sounding of a tuning-fork or a musical string. And, from such a tense vibrating membrane, the vibrations are communicated with great intensity to solid bodies which touch it at any point. If, for example, one end of a flat piece of wood be applied to the membrane of a drum, while the other end is held in the hand, vibrations are felt distinctly when the vibrating tuning-fork is held over the membrane without touching it; but the wood alone, isolated from the membrane, will only very feebly propagate the vibrations of the air to the hand.

In comparing the membrana tympani to the membrane of a drum, it is necessary to point out certain important differences.

When a drum is struck, a certain definite tone is elicited (fundamental tone); similarly a drum is thrown into vibration when certain tones are sounded in its neighbourhood, while it is quite unaffected by others. In other words, it can only take up and vibrate in response to those tones whose vibrations nearly correspond in number with those of its own fundamental tone. The tympanic membrane can take up an immense range of tones produced by vibrations ranging from 30 to 4000 or 5000 per second. This would be clearly impossible if it were an evenly stretched membrane.

The fact is, that the tympanic membrane is by no means evenly stretched, and this is due partly to its slightly funnel-like form, and partly to its being connected with the chain of auditory ossicles. Further, if the membrane were quite free in its centre, it would go on vibrating as a drum does some time after it is struck, and each sound would be prolonged, leading to considerable confusion. This evil is obviated by the ear-bones, which check the continuance of the vibrations like the "dampers" in a pianoforte.

The *ossicula* of the ear are the better conductors of the sonorous vibrations communicated to them, on account of being isolated by an atmosphere of air, and not continuous with the bones of the cranium; for every solid body thus isolated by a different medium, propagates vibrations with more intensity through its own substance than it communicates them to the surrounding medium, which thus prevents a dispersion of the sound; just as the vibrations of the air in the tubes used for conducting the voice from one apartment to another are prevented from being dispersed by the solid walls of the tube. The vibrations of the membrana tympani are transmitted, therefore, by the chain of ossicula to the fenestra ovalis and fluid of the labyrinth, their dispersion in the tympanum being prevented by the difficulty of the transition of vibrations from solid to gaseous bodies.

The necessity of the presence of air on the inner side of the membrana tympani, in order to enable it and the ossicula auditus to fulfil the objects just described, is obvious. Without this provision, neither would the vibrations of the membrane be free, nor the chain of bones isolated, so as to propagate the sonorous undulations with concentration of their intensity. But while the oscillations of the membrana tympani are readily communicated to the air in the cavity of the tympanum, those of the solid ossicula will not be conducted away by the air, but will be propagated to the labyrinth without being dispersed in the tympanum.

The propagation of sound through the ossicula of the tympanum to the labyrinth, must be effected either by oscillations of the bones or by a kind of molecular vibration of their particles, or, most probably, by both these kinds of motion.

Movements of the ossicula.—E. Weber has shown that the existence of the membrane over the fenestra rotunda will permit approximation and removal of the stapes to and from the labyrinth. When by the stapes the membrane of the fenestra ovalis is pressed towards the labyrinth, the membrane of the fenestra rotunda may, by the pressure communicated through the fluid of the labyrinth, be pressed towards the cavity of the tympanum.

The long process of the malleus receives the undulations of the membrana tympani (fig. 364, *a*, *a*) and of the air in a direction indicated by the arrows, nearly perpendicular to itself. From the long process of the malleus they are propagated to its head (*b*): thence into the incus (*c*), the long process of which is parallel with the long process of the malleus. From the long process of the incus the undulations are communicated to the stapes (*d*) which is united to the incus at right angles. The several changes in the direction of the chain of bones have, however, no influence on that of the undulations, which remain the same as it was in the meatus externus and long process of the malleus, so that the undulations are communicated by the stapes to the fenestra ovalis in a perpendicular direction.

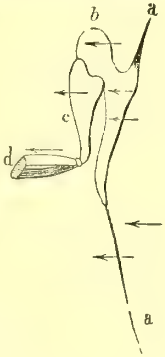


Fig. 364.

Increasing tension of the membrana tympani diminishes the facility of transmission of sonorous undulations from the air to it.

Savart observed that the dry membrana tympani, on the approach of a body emitting a loud sound, rejected particles of sand strewn upon it more strongly when lax than when very tense; and inferred, therefore, that hearing is rendered less acute by increasing the tension of the membrana tympani. Müller has confirmed this by experiments with small membranes arranged so as to imitate the membrana tympani; and it may be confirmed also by observations on one's self.

The pharyngeal orifice of the Eustachian tube is usually shut; during swallowing, however, it is opened; this may be shown as follows:—If the nose and mouth be closed and the cheeks blown out, a sense of pressure is produced in both ears the moment we swallow; this is due, doubtless, to the bulging out of the tympanic membrane by the compressed air which, at that moment, enters the Eustachian tube.

Similarly the tympanic membrane may be pressed in by rarefying the air in the tympanum. This can be readily accomplished by closing the mouth and nose, and making an inspiratory effort and at the same time swallowing (Valsalva). In both cases the sense of hearing is temporarily dulled; proving that equality of pressure on both sides of the tympanic membrane is necessary for its full efficiency.

Functions of Eustachian Tube.—The principal office of the Eustachian tube, in Muller's opinion, has relation to the prevention of these effects of increased tension of the membrana tympani. Its existence and openness will provide for the maintenance of the equilibrium between the air within the tympanum and the external air, so as to prevent the inordinate tension of the membrana tympani which would be produced by too great or too little pressure on either side. While discharging this office, however, it will serve to render sounds clearer, as (Henle suggests) the apertures in violins do; to supply the tympanum with air; and to be an outlet for mucus. If the Eustachian tube were *permanently* open, the sound of one's own voice would probably be greatly intensified, a condition which would of course interfere with the perception of other sounds. At any rate, it is certain that sonorous vibrations can be propagated up the Eustachian tube to the tympanum by means of a tube inserted into the pharyngeal orifice of the Eustachian tube.

Action of Tensor Tympani.—The influence of the tensor tympani muscle in modifying hearing may also be probably explained in connection with the regulation of the tension of the membrana tympani. If, through reflex nervous action, it can be excited to contraction by a very loud sound, just as the iris and orbicularis palpebrarum muscle are by a very intense light, then it is manifest that a very intense sound would, through the action of this muscle, induce a deafening or muffling of the ears. In favour of this supposition we have the fact that a loud sound excites, by reflection, nervous action, winking of the eyelids, and, in persons of irritable nervous system, a sudden contraction of many muscles.

"The ossicula of aquatic mammalia are very bulky and relatively large, especially in the true seals and the sirenia (Manatee and Dugong). In the cetacea the stapes is generally ankylosed to the fenestra ovalis, the malleus is *always* ankylosed to the tympanic bone, yet the membrana tympani is well formed, and there is a manubrium, often ill-developed, but always attached to the membrane by a long process. In the Otariæ or Sea-lions, where the ossicula are far smaller relatively, and less solid than in whales, manatees, and the earless true seals, there are well-formed, movable external ears. The ossicula seem to be vestigial relics utilized for the auditory function. In land animals they vary in shape according to the type of the animal rather than in relation to its acuteness of hearing. I have never found a muscular laxator tympani in any animal, but the tensor exists as a ligament in whales where the malleus is fixed." (Alban Doran.)

Action of the Stapedius.—The influence of the stapedius muscle in hearing is unknown. It acts upon the stapes in such a manner as to make it rest obliquely in the fenestra ovalis depressing that side of it on which it acts, and elevating the other side to the same extent. It prevents too great a movement of the bone.

Functions of the Fluid of the Labyrinth.—*The fluid of the labyrinth* is the most general and constant of the acoustic provisions of the labyrinth. In all forms of organs of hearing, the sonorous vibrations affect the auditory nerve through the medium of liquid—the most convenient medium, on many accounts, for such a purpose.

The *crystalline pulverulent masses* (otoliths) in the labyrinth would reinforce the sonorous vibrations by their resonance, even if they did not actually touch the membranes upon which the nerves are expanded; but, inasmuch as these bodies lie in contact with the membranous parts of the labyrinth, and the vestibular nerve-fibres are imbedded in them, they communicate to these membranes and the nerves, vibratory impulses of greater intensity than the fluid of the labyrinth can impart. This appears to be their office. Sonorous undulations in water are not perceived by the hand itself immersed in the water, but are felt distinctly through the medium of a rod held in the hand. The fine hair-like prolongations from the epithelial cells of the ampullæ have, probably, the same function.

Functions of the Semicircular Canals.—Besides the function of collecting in their fluid contents sonorous undulations from the bones of the cranium, the semicircular canals appear to have another function less directly connected with the sense of hearing. Experiments show that when the horizontal canal is divided in a pigeon a constant movement of the head from side to side occurs, and similarly, when one of the vertical canals is operated upon, up and down movements of the head are observed. These movements are associated, also, with loss of co-ordination, as after the operation the bird is unable to fly in an orderly manner, but flutters and falls when thrown into the air, and, moreover, is able to feed with difficulty. Hearing remains unimpaired. It has been suggested, therefore, that as loss of co-ordination results from section of these canals, and as co-ordinate muscular movements appear to depend to a considerable extent for their due performance upon a correct notion of our equilibrium, that the semicircular canals are connected in some way with this sense, possibly by the constant alterations of the pressure of the fluid within them. The change in the pressure of the fluid in each canal which takes place on any movement of the head, producing sensations which aid in forming an exact judgment of the alteration of position which has occurred.

Functions of the Cochlea.—The *cochlea* seems to be constructed for the spreading out of the nerve-fibres over a wide extent of surface, upon a solid lamina which communicates with the solid walls of the labyrinth and cranium, at the same time that it is in contact with the fluid of the labyrinth, and which, besides exposing the nerve-fibres to the influence of sonorous undulations, by two media, is itself insulated by fluid on either side.

The connection of the lamina spiralis with the solid walls of the labyrinth, adapts the cochlea for the perception of the sonorous undulations propagated by the solid parts of the head and the walls of the labyrinth. The membranous labyrinth of the vestibule and semicircular canals is suspended free in the perilymph, and is destined more particularly for the perception of sounds through the medium of that fluid, whether the sonorous undulations be imparted to the fluid through the fenestræ, or by the intervention of the cranial bones, as when sounding bodies are brought into communication with the head or teeth. The spiral lamina on which the nervous fibres are expanded in the cochlea, is, on the contrary, continuous with the solid walls of the labyrinth, and receives directly from them the impulses which they transmit. This is an important advantage; for the impulses imparted by solid bodies have, *cæteris paribus*, a greater absolute intensity than those communicated by water. And, even when a sound is excited in the water, the sonorous undulations are more intense in the water near the surface of the vessel containing it, than in other parts of the water equally distant from the point of origin of the sound; thus we may conclude that, *cæteris paribus*, the sonorous undulations of solid bodies act with greater intensity than those of water. Hence, we perceive at once an important use of the cochlea.

This is not, however, the sole office of the cochlea; the spiral lamina, as well as the membranous labyrinth, receives sonorous impulses through the medium of the fluid of the labyrinth from the cavity of the vestibule, and from the fenestra rotunda. The lamina spiralis is, indeed, much better calculated to render the action of these undulations upon the auditory nerve efficient, than the membranous labyrinth is; for as a solid body insulated by a different medium, it is capable of resonance.

The *rods of Corti* are probably arranged so that each is set to vibrate in unison with a particular tone, and thus strike a particular note, the sensation of which is carried to the brain by those filaments of the auditory nerve with which the little vibrating rod is connected. The distinctive function, therefore, of these minute bodies is, probably, to render sensible to the brain the various musical notes and tones, one of them answering to one tone, and one to another; while perhaps the other parts of the organ of hearing discriminate between the intensities of different sounds, rather than their qualities.

"In the cochlea we have to do with a series of apparatus adapted for performing sympathetic vibrations with wonderful exactness. We have here before us a musical instrument which is designed, not to create musical sounds, but to render them perceptible, and which is similar in construction to artificial musical instruments, but which far surpasses them in the delicacy as well as the simplicity of its execution. For, while in a piano every string must have a separate hammer by means of which it is sounded, the ear possesses a single hammer of an ingenious form in its ear-bones, which can make every string of the organ of Corti sound separately." (Bernstein.)

About 3000 rods of Corti are present in the human ear; this would give about 400 to each of the seven octaves which are within the compass of the ear. Thus about 32 would go to each semi-*tone*. Weber asserts that accomplished musicians can appreciate differences in pitch as small as $\frac{1}{64}$th of a tone. Thus on the theory above advanced, the delicacy of discrimination would, in this case, appear to have reached its limits.

Sensibility of the Auditory Nerve.—Any elastic body, *e.g.*, air, a membrane, or a string performing a certain number of regular vibrations in the second, gives rise to what is termed a musical sound or *tone*. We must, however, distinguish between a musical sound and a mere noise; the latter being due to irregular vibrations.

Qualities of Musical Sound.—Musical sounds are distinguished from each other by three qualities. 1. *Strength* or intensity, which is due to the amplitude or length of the vibrations. 2. *Pitch*, which depends upon the number of vibrations in a second. 3. *Quality*, *Colour*, or *Timbre*. It is by this property that we distinguish the same note sounded on two instruments, *e.g.*, a piano and a flute. It has been proved by Helmholtz to depend on the number of secondary notes, termed *harmonics*, which are present with the predominating or fundamental tone.

It would appear that two impulses, which are equivalent to four single or half vibrations, are sufficient to produce a definite note, audible as such through the auditory nerve. The note produced by the shocks of the teeth of a revolving wheel, at regular intervals upon a solid body, is still heard when the teeth of the wheel are removed in succession, until two only are left; the second produced by the impulse of these two teeth has still the same definite value in the scale of music.

The maximum and minimum of the intervals of successive impulses still appreciable through the auditory nerve as determinate sounds, have been determined by M. Savart. If their intensity is sufficiently great, sounds are still audible which result from the succession of 48,000 half vibrations, or 24,000 impulses in a second; and this, probably, is not the extreme limit in acuteness of sounds perceptible by the ear. For the opposite extreme, he has succeeded in rendering sounds audible which were produced by only fourteen or eighteen half vibrations, or seven or eight impulses in a second; and sounds still deeper might probably be heard, if the individual impulses could be sufficiently prolonged

By removing one or several teeth from the toothed wheel the fact has been demonstrated that in the case of the auditory nerve, as in that of the optic nerve, the sensation continues longer than the impression which causes it; for a removal of a tooth from the wheel produced no interruption of the sound. The gradual cessation of the sensation of sound renders it difficult, however, to determine its exact duration beyond that of the impression of the sonorous impulses.

Direction of Sounds.—The power of perceiving the *direction of* *sounds* is not a faculty of the sense of hearing itself, but is an act of the mind judging on experience previously acquired. From the modifications which the sensation of sound undergoes according to the direction in which the sound reaches us, the mind infers the position of the sounding body. The only true guide for this inference is the more intense action of the sound upon one than upon the other ear. But even here there is room for much deception, by the influence of reflexion or resonance, and by the propagation of sound from a distance, without loss of intensity, through curved conducting tubes filled with air. By means of such tubes, or of solid conductors, which convey the sonorous vibrations from their source to a distant resonant body, sounds may be made to appear to originate in a new situation. The direction of sound may also be judged of by means of one ear only; the position of the ear and head being varied, so that the sonorous undulations at one moment fall upon the ear in a perpendicular direction, at another moment obliquely. But when neither of these circumstances can guide us in distinguishing the direction of sound, as when it falls equally upon both ears, its source being, for example, either directly in front or behind us, it becomes impossible to determine whence the sound comes.

Distance of Sounds.—The *distance of the source of sounds* is not recognized by the sense itself, but is inferred from their intensity. The sound itself is always seated but in one place, namely, in our ear; but it is interpreted as coming from an exterior soniferous body. When the intensity of the voice is modified in imitation of the effect of distance, it excites the idea of its originating at a distance. Ventriloquists take advantage of the difficulty with which the direction of sound is recognized, and also the influence of the imagination over our judgment, when they direct their voice in a certain direction, and at the same time pretend, themselves, to hear the sounds as coming from thence.

The effect of the action of sonorous undulations upon the nerve of hearing, endures somewhat longer than the period during which the undulations are passing through the ear. If, however, the impressions of the same sound be very long continued, or constantly repeated for a long time, then the sensation produced may continue for a very long time, more than twelve or twenty-four hours even, after the original cause of the sound has ceased.

Binaural Sensations.—Corresponding to the double vision of the same object with the two eyes, is the double hearing with the two ears; and analogous to the double vision with one eye, dependent on unequal refraction, is the double hearing of a single sound with one ear, owing to the sound coming to the ear through media of unequal conducting power. The first kind of double hearing is very rare; instances of it are recorded, however, by Sauvages and Itard. The second kind, which depends on the unequal conducting power of two media through which the same sound is transmitted to the ear, may easily be experienced. If a small bell be sounded in water, while the ears are closed by plugs, and a solid conductor be interposed between the water and the ear, two sounds will be heard differing in intensity and tone; one being conveyed to the ear through the medium of the atmosphere, the other through the conducting-rod.

Subjective Sensations of Sound.—*Subjective sounds* are the result of a state of irritation or excitement of the auditory nerve produced by other causes than sonorous impulses. A state of excitement of this nerve, however induced, gives rise to the sensation of sound. Hence the ringing and buzzing in the ears heard by persons of irritable and exhausted nervous system, and by patients with cerebral disease, or disease of the auditory nerve itself; hence also the noise in the ears heard for some time after a long journey in a rattling noisy vehicle. Ritter found that electricity also excites a sound in the ears. From the above truly subjective sound we must distinguish those dependent, not on a state of the auditory nerve itself merely, but on sonorous vibrations excited in the auditory apparatus. Such are the buzzing sounds attendant on vascular congestion of the head and ear, or on aneurismal dilatation of the vessels. Frequently even the simple pulsatory circulation of the blood in the ear is heard. To the sounds of this class belong also the buzz or hum heard during the contraction of the palatine muscles in the act of yawning; during the forcing of air into the tympanum, so as make tense the membrana tympani; and in the act of blowing the nose, as well during the forcible depression of the lower jaw.

Irritation or excitement of the auditory nerve is capable of giving rise to movements in the body, and to sensations in other organs of sense. In both cases it is probable that the laws of reflex action, through the medium of the brain, came into play. An intense and sudden noise excites, in every person, closure of the eyelids, and, in nervous individuals, a start of the whole body or an unpleasant sensation, like that produced by an electric shock, throughout the body, and sometimes a particular feeling in the external ear. Various sounds cause in many people a disagreeable feeling in the teeth, or a sensation of cold tickling through the body, and, in some people, intense sounds are said to make the saliva collect.

Sight.

Eyelids and Lachrymal Apparatus.—The *eyelids* consist of two movable folds of skin, each of which is kept in shape by a thin plate of yellow elastic tissue. Along their free edges are inserted a number of curved hairs (*eyelashes*), which, when the lids are half closed, serve to protect the eye from dust and other foreign bodies: their tactile sensibility is also very delicate.

On the inner surface of the elastic tissue are disposed a number of small racemose glands (Meibomian), whose ducts open near the free edge of the lid.

The orbital surface of each lid is lined by a delicate, highly sensitive mucous membrane (*conjunctiva*), which is continuous with the skin at the free edge of each lid, and after lining the inner surface of the eyelid is reflected on to the eyeball, being somewhat loosely adherent to the sclerotic coat. The epithelial layer is continued over the cornea at its anterior epithelium. At the inner edge of the eye the conjunctiva becomes continuous with the mucous lining of the lachrymal sac and duct, which again is continuous with the mucous membrane of the inferior meatus of the nose.

The *lachrymal gland* is lodged in the upper and outer angle of the orbit. Its secretion, which issues from several ducts on the inner surface of the upper lid, under ordinary circumstances just suffices to keep the conjunctiva moist. It passes out through two small openings (puncta lachrymalia) near the inner angle of the eye, one in each lid, into the lachrymal sac, and thence along the nasal duct into the inferior meatus of the nose The excessive secretion poured out under the influence of any irritating vapour or painful emotion overflows the lower lid in the form of tears.

The eyelids are closed by the contraction of a sphincter muscle (*orbicularis*), supplied by the Facial nerve; the upper lid is raised by the *Levator palpebræ superioris*, which is supplied by the Third nerve.

The Eyeball.

The eyeball or the organ of vision (fig. 365) consists of a variety of structures which may be thus enumerated:—

The *sclerotic*, or outermost coat, envelops about five-sixths of the eyeball: continuous with it, in front, and occupying the remaining sixth is the *cornea*. Immediately within the sclerotic is the *choroid* coat, and within the choroid is the *retina*. The interior of the eyeball is well-nigh filled by the *aqueous* and *vitreous humours* and the *crystalline lens;* but, also, there is suspended in the interior a contractile and perforated curtain,—the *iris*, for regulating the admission of light, and behind the junction of the sclerotic and cornea is a ciliary muscle, the function of which is to adapt the eye for seeing objects at various distances.

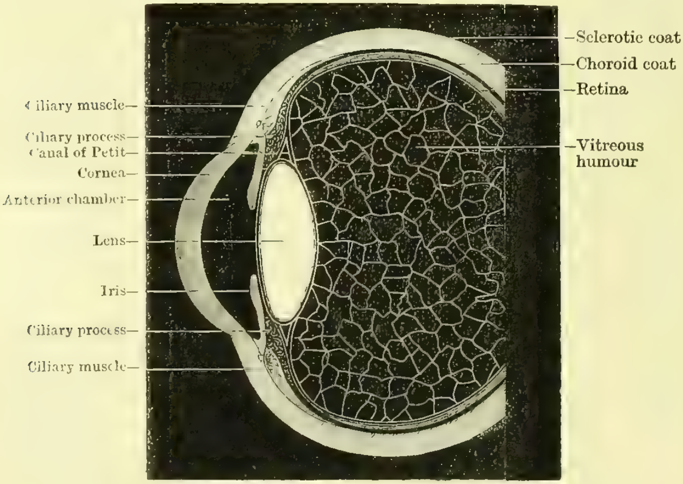


Fig. 365.

Structure of Sclerotic.—The *sclerotic* coat is composed of connective tissue, arranged in variously disposed and inter-communicating layers. It is strong, tough, and opaque, and not very elastic.

Structure of Cornea.—The *cornea* is a transparent membrane which forms a segment of a smaller sphere than the rest of the eyeball, and is let in, as it were, into the sclerotic with which it is continuous all round. It is coated with a laminated anterior epithelium (*a*, fig. 367) consisting of seven or eight layers of cells, of which the superficial ones are flattened and scaly, and the deeper ones more or less columnar. Immediately beneath this is the anterior elastic lamina (Bowman).

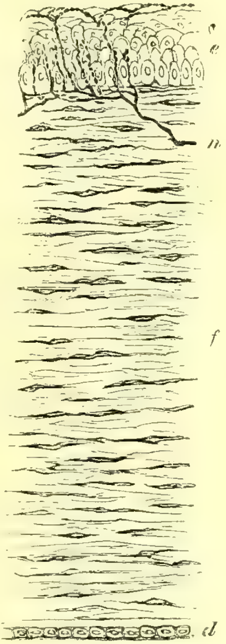


Fig. 366.—*Vertical section of rabbit's cornea*, stained with gold chloride. *e*, Laminated anterior epithelium. Immediately beneath this is the anterior elastic lamina of Bowman. *n*, Nerves forming a delicate sub-epithelial plexus, and sending up fine twigs between the epithelial cells to end in a second plexus on the free surface; *d*, Descemet's membrane, consisting of a fine elastic layer, and a single layer of epithelial cells; the substance of the cornea, *f*, is seen to be fibrillated, and contains many layers of branched corpuscles, arranged parallel to the free surface, and here seen edgewise. (Schofield.)

The cornea tissue proper as well as its epithelium is, in the adult, completely destitute of blood-vessels; it consists of an intercellular ground-substance of rather obscurely fibrillated flattened bundles of connective tissue, arranged parallel to the free surface, and forming the boundaries of branched anastomosing spaces in which the cornea-corpuscles lie. These branched cornea-corpuscles have been seen to creep by amœboid movement from one branched space into another. At its posterior surface the cornea is limited by the posterior elastic lamina, or membrane of Descemet, the inner layer of which consists of a single stratum of epithelial cells (fig. 366, *d*).

Nerves of Cornea.—The nerves of the cornea are both large and numerous: they are derived from the ciliary nerves. They traverse the substance of the cornea, in which some of them terminate, in the direction of its anterior surface, near which the axis cylinders break up into bundles of very delicate beaded fibrillæ (fig. 366): these form a plexus immediately beneath the epithelium, from which delicate fibrils pass up between the cells anastomosing with horizontal branches, and forming a deep intra-epithelial plexus, from which fibres ascend, till near the surface they form a superficial intra-epithelial net-work.

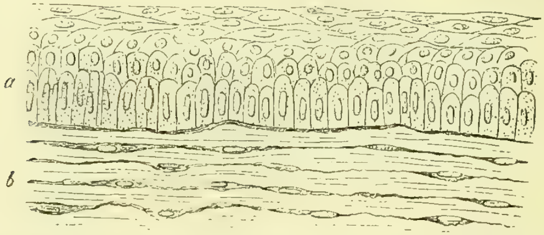


Fig. 367.—*Vertical section of rabbit's cornea.* *a*, Anterior epithelium, showing the different shapes of the cells at various depths from the free surface; *b*, portion of the substance of cornea. (Klein.)

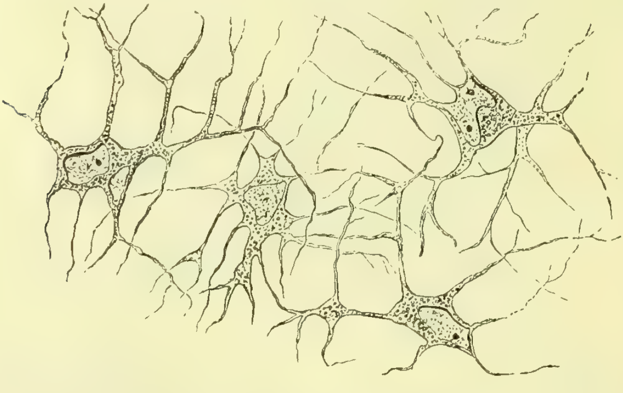


Fig. 368.—*Horizontal preparation of cornea of frog;* showing the network of branched cornea corpuscles. The ground substance is completely colourless. × 400. (Klein.)

Structure of Choroid (*tunica vasculosa*).—This coat of the eye-ball is formed by a very rich network of capillaries (choriocapillaris) outside which again are connective-tissue layers of stellate pigmented cells (fig. 25) with numerous arteries and veins.

The choroid coat ends in front in what are called the *ciliary processes* (fig. 365).

Structure of Retina.—The *retina* (fig. 370) is a delicate membrane, concave, with the concavity directed forwards and ending in front, near the outer part of the ciliary processes in a finely notched edge,—the *ora serrata.* Semi-transparent when fresh, it soon becomes clouded and opaque, with a pinkish tint from the blood in its minute vessels. It results from the sudden spreading out or expansion of the optic nerve, of whose terminal fibres, apparently deprived of their external white substance, together with nerve cells, it is essentially composed.

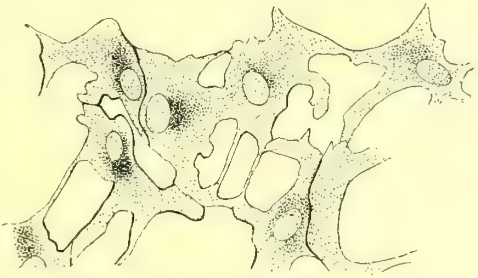


Fig. 369.—*Surface view of part of lamella of kitten's cornea*, prepared first with caustic potash and then with nitrate of silver. By this method the branched cornea-corpuscles with their granular protoplasm and large oval nuclei are brought out.) × 450. (Klein and Noble Smith.)

Exactly in the centre of the retina, and at a point thus corresponding to the axis of the eye in which the sense of vision is most perfect, is a round yellowish elevated spot, about $\frac{1}{24}$ of an inch in diameter, having a minute aperture at its summit, and called after its discoverer the *yellow spot of Sœmmering.* In its centre is a minute depression called *fovea centralis.* About $\frac{1}{10}$ of an inch to the inner side of the yellow spot, and consequently of the axis of the eye, is the point at which the optic nerve begins to spread out its fibres to form the retina. This is the only point of the surface of the retina from which the power of vision is absent.

The retina consists of certain nervous elements arranged in several layers, and supported by a very delicate connective tissue.

From the nature of the case there is still considerable uncertainty as to the character (nervous or connective tissue) of some of the layers of the retina. The following ten layers, from within outwards, are usually to be distinguished in a vertical section (figs. 370, 373).

1. *Membrana limitans interna:* a delicate membrane in contact with the vitreous humour.

2. *Fibres of optic nerve.* This layer is of very varying thickness in different parts of the retina: it consists chiefly of non-medullated

fibres which interlace, and some of which are continuous with processes of the large nerve-cells forming the next layer.

3. *Layer of ganglionic corpuscles*, consisting of large multipolar nerve-cells, sometimes forming a single layer. In some parts of the retina, especially near the *macula lutea*, this layer is very thick, consisting of several distinct strata of nerve-cells. These cells lie in the spaces of a connective-tissue framework.

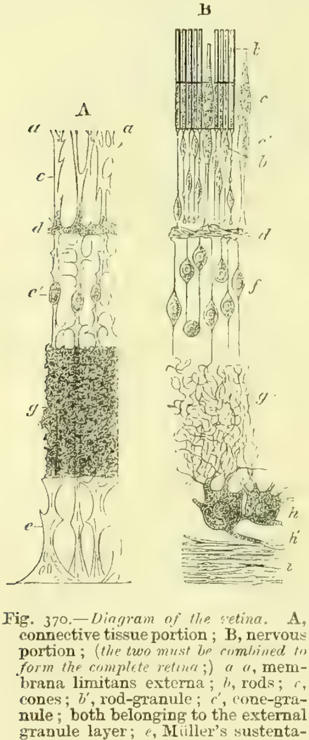


Fig. 370.—*Diagram of the retina.* A, connective tissue portion; B, nervous portion; (*the two must be combined to form the complete retina*;) *a a*, membrana limitans externa; *b*, rods; *c*, cones; *b'*, rod-granule; *c'*, cone-granule; both belonging to the external granule layer; *e*, Müller's sustentacular fibres, with their nuclei *e'*; *d*, intergranular layer; *f*, internal granule layer; *g*, molecular layer, connective-tissue portion; *g'*, molecular layer, nerve-fibril portion; *h*, ganglion cells; *h'*, their axis-cylinder process; *i*, nerve-fibre layer. (Max Schultze.)

4. *Molecular layer.* This presents a finely granulated appearance. It consists of a punctiform connective tissue traversed by numberless very fine fibrillar processes of the nerve-cells.

5. *Internal granular layer.* This consists chiefly of numerous small round cells with a very small quantity of protoplasm surrounding a large nucleus; they are generally bipolar, giving off one process outwards and another inwards. They greatly resemble the ganglionic corpuscles of the cerebellum (fig. 330). Besides these there are large oval nuclei (é, fig. 370, A) belonging to the sustentacular connective tissue fibres.

6. *Intergranular layer;* which closely resembles the molecular layer but is much thinner. It consists of finely-dotted connective tissue with nerve fibrils.

7. *External granular layer;* which consists of several strata of small cells resembling those of the internal granular layer; they have been classed as rod and cone granules, according as they are connected by very delicate fibrils with the rods and cones respectively. They are lodged in the meshes of a connective

tissue framework. Both the internal and external granular layer stain very rapidly and deeply with hæmatoxylin, while the rod and cone layer remains quite unstained.

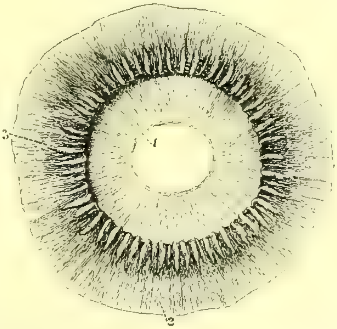


Fig. 371.—*Ciliary processes*, as seen from behind. 1, posterior surface of the iris, with the sphincter muscle of the pupil; 2, anterior part of the choroid coat; 3, one of the ciliary processes, of which about seventy are represented. ½.

8. *Membrana limitans externa*; a delicate, well-defined membrane, clearly marking the internal limit of the rod and cone layer.

9. *Rod and cone layer, bacillar layer, or membrane of Jacob*, consisting of two kinds of elements: the "rods," which are cylindrical and of uniform diameter throughout, and the "cones," whose internal portion is distinctly conical, and surmounted externally by a thin rod-like body. According to the researches of Max Schultze, the rods show traces of longitudinal fibrillation, and, moreover, have a great tendency to break up into a number of transverse discs like a pile of coins.

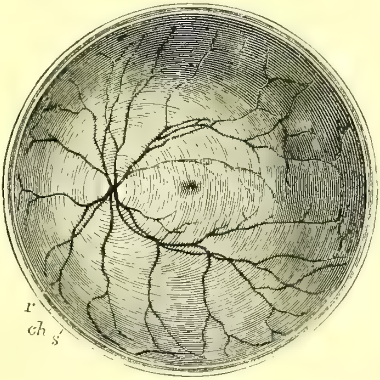


Fig. 372.—*The posterior half of the retina of the left eye*, viewed from before; *s*, the cut edge of the sclerotic coat; *ch*, the choroid; *r*, the retina; in the interior at the middle, the macula lutea with the depression of the fovea centralis is represented by a slight oval shade; towards the left side the light spot indicates the colliculus or eminence at the entrance of the optic nerve, from the centre of which the arteria centralis is seen spreading its branches into the retina, leaving the part occupied by the macula comparatively free. (After Henle.)

In the rod and cone layer of birds, the cones usually predominate largely in number, whereas in man the rods are by far the more numerous. In nocturnal birds, however, such as the owl, only rods are present, and the same appears to be the case in many nocturnal and burrowing mammalia, *e.g.*, bat, hedge-hog, mouse, and mole.

10. *Pigment cell layer*, which was formerly considered part of the choroid.

In the centre of the yellow spot (macula lutea), all the layers of the retina become greatly thinned out and almost disappear, except the rod and cone layer, which considerably increases in thickness, and comes to consist almost entirely of long slender cones, the rods being very few in number, or entirely absent. There are capillaries here, but none of the larger branches of the retinal arteries.

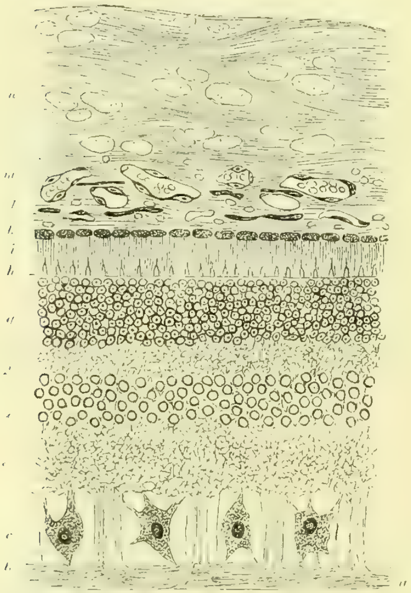


Fig. 373.—*Section of the retina, choroid, and part of the sclerotic*, moderately magnified. *a*, membrana limitans interna; *b*, nerve-fibre layer traversed by Müller's sustentacular fibres (of the connective tissue system); *c*, ganglion-cell layer; *d*, molecular layer; *e*, internal granular layer; *f*, intergranular layer; *g*, external granular layer; *h*, membrana limitans externa, running along the lower part of *i*, the layer of rods and cones; *k*, pigment cell layer formerly described as part of the choroid; *l*, *m*, internal and external vascular portions of the choroid, the first containing capillaries, the second larger blood-vessels, cut in transverse section; *n*, sclerotic. (W. Pye.)

With regard to the connection of the various layers there is still some uncertainty. Fig. 370 represents the view of Max Schultze. According to this there are certain sustentacular fibres of connective tissue (radiating fibres of Müller) which spring from the *membrana limitans interna* almost vertically, and traverse the retina to the *limitans externa*, whence very delicate connective tissue processes pass up between the rods and cones. The framework which they form is represented in fig. 370, A. The *nervous* elements of the retina are represented in fig. 370, B, and consist of delicate fibres passing up from the nerve-fibre layer to the rods and cones, and connected with the ganglionic corpuscles and granules of the internal and external layer.

Blood-vessels of the Eyeball.—The eye is very richly supplied with blood-vessels. In addition to the conjunctival vessels which are derived from the palpebral and lachrymal arteries, there are at least two other distinct sets of vessels supplying the tunics of the eyeball. (1) The vessels of the sclerotic, choroid, and iris, and (2) The vessels of the retina.

(1.) These are the short and long *posterior* ciliary arteries which pierce the sclerotic in the posterior half of the eyeball, and the *anterior* ciliary which enter near the insertions of the recti. These vessels anastomose and form a very rich choroidal plexus; they also supply the iris and ciliary processes, forming a very highly vascular circle round the outer margin of the iris and adjoining portion of the sclerotic.

The distinctness of these vessels from those of the conjunctiva is well seen in the difference between the bright red of blood-shot eyes (conjunctival congestion), and the pink zone surrounding the cornea which indicates deep-seated ciliary congestion.

(2.) The *retinal vessels* (fig. 372) are derived from the *arteria centralis retinæ*, which enters the eyeball along the centre of the optic nerve. They ramify all over the retina, chiefly in its inner layers. They can be seen by direct ophthalmoscopic examination.

Optical Apparatus.

The eye may be compared to the *camera* used by photographers formed by a convex lens. In this instrument images of external objects are thrown upon a ground-glass screen at the back of a box, the interior of which is painted black. In the eye the convex lens is represented by the crystalline lens, the dark box by the eye-ball with its choroidal pigment, and the screen by the retina. In the case of the camera the screen is enabled to receive clear images of objects at different distances, by being shifted forward and back: while the convex lens too can be screwed in and out. The corresponding contrivance in the eye will be described under the head of *Accommodation*.

Conditions Necessary.—The essential constituents of the optical apparatus of the eye may be thus enumerated: (1) A *nervous* structure (the retina) to be stimulated by light and to transmit by means of the optic nerve, of which it is the terminal expansion, the impression of the stimulation to the brain, in which it excites the sensation of vision; (2) An *apparatus* consisting of certain refractory media, cornea, crystalline lens, aqueous and vitreous humour, the function of which is to collect together into one point, the different divergent rays emitted by each point of every external body and of giving them such directions that they are exactly focussed upon the retina, and thus produce an exact image of the object from which they proceed. For as light radiates from a luminous body in all directions, when the media offer no impediment to its transmission, a luminous point will necessarily illuminate all parts of a surface, such as the retina opposed to it, and not merely one single point. A retina, therefore, without any optical apparatus placed in front of it to separate the light of different objects, would not allow of distinct vision, but would merely transmit such a general impression of daylight as would distinguish it from the night; (3) A contractile *diaphragm* (iris) with a central aperture for regulating the quantity of light admitted into the eye; and (4) a contractile structure (ciliary muscle), an arrangement by which the chief refracting medium (crystalline lens) shall be so controlled as to enable objects to be seen at various distances, causing convergence of the rays of light that fall upon and traverse it (accommodation).

Refracting Media.

Of the refracting media the *cornea* is in a twofold manner capable of refracting and causing convergence of the rays of light that fall upon and traverse it. It thus affects them first, by its density; for it is a law in optics that when rays of light pass from a rarer into a denser medium, if they impinge upon the surface in a direction removed from the perpendicular, they are bent out of their former direction towards that of a line perpendicular to the surface of the denser medium; and, secondly, by its convexity; since rays of light impinging upon a convex transparent surface, are refracted towards the centre, those being most refracted which are farthest from the centre of the convex surface.

Behind the cornea is a space containing a thin watery fluid, the *aqueous humour*, holding in solution a small quantity of sodium chloride and extractive matter. The space containing the aqueous humour is divided into an anterior and posterior *chamber* by a membranous partition, *the iris*, to be presently again mentioned. The effect produced by the aqueous humour on the rays of light traversing it, is not yet fully ascertained. Its chief use, probably, is to assist in filling the eyeball, so as to maintain its proper convexity, and at the same time to furnish a medium in which the movements of the iris can take place.

Behind the aqueous humour and the iris, and imbedded in the anterior part of the medium next to be described, viz., the vitreous humour, is seated a doubly-convex body, the *crystalline lens*, which is the most important refracting structure of the eye. The structure of the lens is very complex. It consists essentially of fibres united side by side to each other, and arranged together in very numerous laminæ, which are so placed upon one another, that when hardened in spirit the lens splits into three portions in the form of sectors, each of which is composed of superimposed concentric laminæ. The lens increases in density and, consequently, in power of refraction, from without inwards; the central part, usually termed the nucleus, being the most dense.

The *vitreous humour* constitutes nearly four-fifths of the whole globe of the eye. It fills up the space between the retina and the lens, and its soft jelly-like substance consists essentially of numerous layers, formed of delicate, simple membrane, the spaces between which are filled with a watery, pellucid fluid. Its principal use appears to be that of giving the proper distension to the globe of the eye, and of keeping the surface of the retina at a proper distance from the lens.

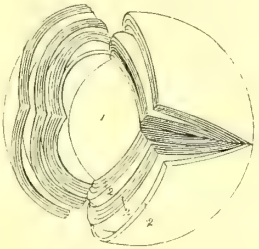


Fig. 374.—*Laminated structure of the crystalline lens.* The laminæ are split up after hardening in alcohol. 1, the denser central part or nucleus; 2, the successive external layers. $\frac{4}{1}$. (Arnold.)

Action of the Iris.—The *iris* is a vertically-placed membranous diaphragm, provided with a central aperture, the *pupil*, for the transmission of light. It is composed of plain muscular fibres imbedded in ordinary fibro-cellular or connective tissue. The muscular fibres have a direction, for the most part, radiating from the circumference towards the pupil; but as they approach the pupillary margin, they assume a circular direction, and at the very edge form a complete ring. By the contraction of the radiating fibres (dilator pupillæ) the size of the pupil is enlarged: by the contraction of the circular ones (sphincter pupillæ), it is diminished. The object effected by the movements of the iris, is the regulation of the quantity of light transmitted to the retina. The posterior surface of the iris is coated with a layer of dark pigment, so that no rays of light can pass to the retina, except such as are admitted through the aperture of the pupil.

This iris is very richly supplied with nerves and blood-vessels. Its circular muscular fibres are supplied by the third (by the short ciliary branches of the ophthalmic ganglion), and its radiating fibres, by the sympathetic and fifth cranial nerve (by the long ciliary branches of the nasal nerve).

Contraction of the pupil occurs under the following circumstances: (1) On exposure of the eye to a bright light; (2) when the eye is focussed for near objects; (3) when the eyes converge to look at a near object; (4) on the local application of eserine (active principle of Calabar bean); (5) on the administration internally of opium, aconite, and in the early stages of chloroform and alcohol poisoning; (6) on division of the cervical sympathetic or stimulation of the third nerve. *Dilatation* of the pupil occurs (1) in a dim light; (2) when the eye is focussed for distant objects; (3) on the local application of atropine and its allied alkaloids; (4) on the internal administration of atropine and its allies; (5) in the later stages of poisoning by chloroform, opium, and other drugs; (6) on paralysis of the third nerve; (7) on stimulation of the cervical sympathetic, or of its centre in the floor of the front of the aqueduct of Sylvius. The contraction of the pupil appears to be under the control of a centre in the corpora quadrigemina, and this is reflexly stimulated by a bright light, and the dilatation when the reflex centre is not in action is due to the more powerful sympathetic action; but in addition, it appears that both contraction and dilatation may be produced by a local mechanism, upon which certain drugs can act, which is independent of and probably often antagonistic to the action of the central apparatus of the third and sympathetic nerves. The action of the fifth nerve upon the pupil is not well understood, but its apparent effect in producing dilatation is due to the mixture of sympathetic fibres with its nasal branch. The sympathetic influence upon the radiating fibres is believed to be conveyed not by the long ciliary branches of that nerve, but by the short ciliary branches from the ophthalmic ganglion.

The close sympathy subsisting between the two eyes is nowhere better shown than by the condition of the pupil. If one eye be shaded by the hand its pupil will of course dilate; but the pupil of the *other* eye will also dilate, though it is unshaded.

Ciliary Muscle.—The *ciliary muscle* is composed of plain muscular fibres, which form a narrow zone around the interior of the eyeball, near the line of junction of the cornea with the sclerotic, and just behind the outer border of the iris (fig. 365). The *outermost* fibres of this muscle are attached in front to the inner part of the sclerotic and cornea at their line of junction, and diverging somewhat, are fixed to the ciliary processes, and a small portion of the choroid immediately behind them. The *inner* fibres immediately within the preceding, form a circular zone around the interior of the eyeball, outside the ciliary processes. They compose the ring formerly called the ciliary ligament.

Accommodation of the Eye.—The distinctness of the image formed upon the retina, is mainly dependent on the rays emitted by each luminous point of the object being brought to a perfect focus upon the retina. If this focus occur at a point either in front of, or behind the retina, indistinctness of vision ensues, with the production of a halo. The *focal distance*, *i.e.*, the distance of the point at which the luminous rays from a lens are collected, besides being regulated by the degree of convexity and density of the lens, varies with the distance of the object from the lens, being greater as this is shorter, and *vice versâ*. Hence, since objects placed at various distances from the eye can, within a certain range, different in different persons, be seen with almost equal distinctness, there must be some provision by which the eye is enabled to adapt itself, so that whatever length the focal distance may be, the focal point may always fall exactly upon the retina.

This power of *adaptation of the eye to vision at different distances* has received the most varied explanations. It is obvious that the effect might be produced in either of two ways, viz., by altering the convexity or intensity, and thus the refracting power, either of the cornea or lens ; or by changing the position either of the retina or of the lens, so that whether the object viewed be near or distant, and the focal distance thus increased or diminished, the focal point to which the rays are converged by the lens may always be at the place occupied by the retina. The amount of either of these changes required in even the widest range of vision, is extremely small. For, from the refractive powers of the media of the eye, it has been calculated by Olbers, that the difference between the focal distances of the images of an object at such a distance that the rays are parallel, and of one at the distance of four inches, is only about 0·143 of an inch. On this calculation, the change in the distance of the retina from the lens required for vision at all distances, supposing the cornea and lens to maintain the same form, would not be more than about one line.

It is now almost universally believed that Helmholtz is right in his statement that the immediate cause of the adaptation of the eye for objects at different distances is a varying shape of the lens, its front surface becoming more or less convex, according to the distance of the object looked at. The nearer the object, the more convex does the front surface of the lens become, and *vice versâ ;* the back surface taking little or no share in the production of the effect required. The following simple experiment illustrates this point. If a small flame be held little to one side of a person's eye, an observer looking at the eye from the other side sees three distinct images of the flame (fig. 375). The first and brightest is (1) a small erect image formed by the anterior convex surface of the cornea : the second (2) is also erect, but larger and less distinct than the preceding, and is formed at the anterior convex surface of the lens : the third (3) is smaller and reversed, it is formed at the posterior surface of the lens, which is concave forwards, and therefore, like all concave mirrors, gives a reversed image. If now the eye under observation be made to look at a near object, the second image becomes smaller, clearer, and approaches the

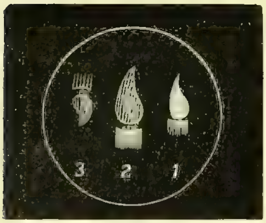


Fig. 375.—*Diagram showing three reflections of a candle.* 1, From the anterior surface of cornea; 2, from the anterior surface of lens; 3, from the posterior surface of lens. For further explanation, see text. The experiment is best performed by employing an instrument invented by Helmholtz, termed a *Phakoscope.*

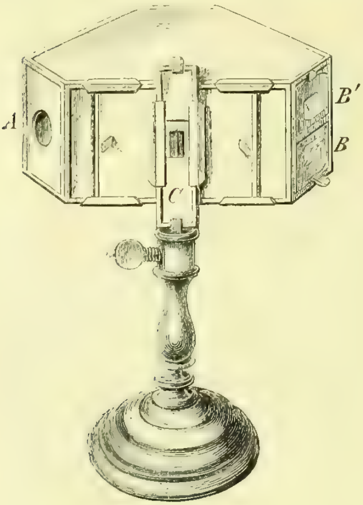


Fig. 376.—*Phakoscope of Helmholtz.* At *B B'* are two prisms, by which the light of a candle is concentrated on the eye of the person experimented with at *C; A* is the aperture for the eye of the observer. The observer notices three double images, as in fig. 375, reflected from the eye under examination when the eye is fixed upon a distant object; the position of the images having been noticed the eye is then made to focus a near object, such as a needle pushed up by *C;* the images from the anterior surface of the lens will be observed to move towards each other, in consequence of the lens becoming more convex.

first. If the eye be now adjusted for a far point, the second image enlarges again, becomes less distinct, and recedes from the first. In both cases alike the first and third images remain unaltered in size and relative position. This proves that during accommodation for near objects the curvature of the cornea, and of the *posterior* of the lens, remains unaltered, while the *anterior* surface of the lens becomes more convex and approaches the cornea.

Mechanism of Accommodation.—Of course the lens has no inherent power of contraction, and therefore its changes of outline must be produced by some power from without; and there seems no reason to doubt that this power is supplied by the ciliary muscle. It is sometimes termed the *tensor choroideæ.* As this name implies, from its attachment (p. 702), it is able to draw forwards the choroid, and therefore slackens the tension of the suspensory ligament of the lens which arises from it. The lens is usually partly flattened by the action of the suspensory ligament; and the ciliary muscle by diminishing the tension of this ligament diminishes, to a proportional degree, the flattening of which it is the cause. On diminution or cessation of the action of the ciliary muscle, the lens returns, in a corresponding degree, to its former shape, by virtue of the elasticity of its suspensory ligament (fig. 377). From this it will appear that the eye is usually focussed for distant objects. In viewing near objects the pupil contracts, the opposite effect taking place on withdrawal of the attention from near objects, and fixing it on those distant.

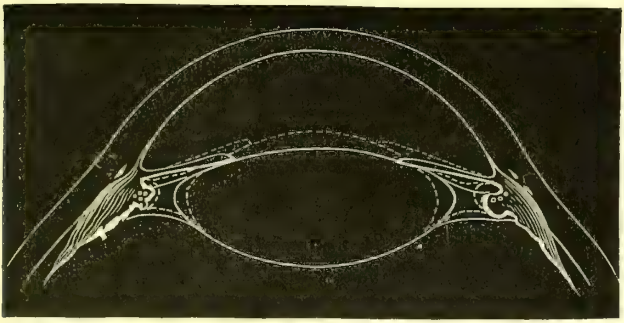


Fig. 377.—*Diagram representing by dotted lines the alteration in the shape of the lens, on accommodation for near objects.* (E. Landolt.)

Range of Distinct Vision. Near-point.—In every eye there is a limit to the power of accommodation. If a book be brought nearer and nearer to the eye, the type at last becomes indistinct and cannot be brought into focus by any effort of accommodation, however strong. This, which is termed the *near-point*, can be determined by the following experiment (*Scheiner*). Two small holes are pricked in a card with a pin not more than a line apart, at any rate their distance from each other must not exceed the diameter of the pupil. The card is held close in front of the eye, and a small needle viewed through the pin-holes. At a moderate distance it can be clearly focussed, but when brought nearer, beyond a certain point, the image appears double or at any rate blurred. This point where the needle ceases to appear single is the near-point. Its distance from the eye can of course be readily measured. It is usually about 5 or 6 inches. In the accompanying figure (fig. 378) the lens *b* represents the eye; *ef* the two pinholes in the card, *nn* the retina; *a* represents the position of the needle. When the needle is at a moderate distance, the two pencils of light coming from *e* and *f*, are focussed at a single point on the retina *nn*. If the needle be brought nearer than the near-point, the strongest effort of accommodation is not sufficient to focus the two pencils, they meet at a point behind the retina. The effect is the same as if the retina were shifted forward to *mm*. Two images, *h*, *g*, are formed, one from each hole. It is interesting to note that when two images are produced, the lower one *g* really appears in the position Q, while the upper one appears in the position P. This may be readily verified by covering the holes in succession.

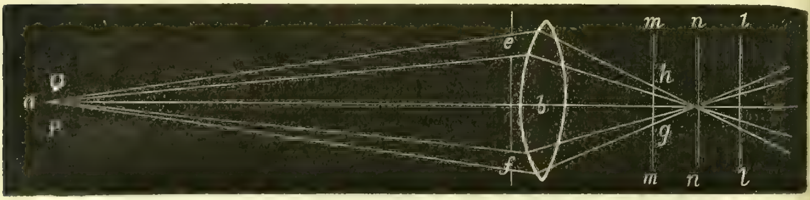


Fig. 378.—*Diagram of experiment to ascertain the minimum distance of distinct vision.*

The contents of the ball of the eye are surrounded and kept in position by the *cornea*, and the dense, fibrous membrane before referred to as the *sclerotic*, which, besides thus encasing the contents of the eye, serves to give attachment to the various muscles by which the movements of the eye-ball are effected. These muscles, and the nerves supplying them, have been already considered (p. 620, *et seq.*).

Course of a Ray of Light.—With the help of the diagram (fig. 379) representing a vertical section of the eye from before backwards, the mode in which, by means of the refracting media of the eye, an image of an object of sight is thrown on the retina, may be rendered intelligible. The rays of the cones of light emitted by the points A B, and every other point of an object placed before the eye, are first refracted, that is, are bent towards the axis of the cone, by the cornea C C, and the aqueous humour contained between it and the lens. The rays of each cone are again refracted and bent still more towards its central ray or axis by the anterior surface of the lens E E; and again as they pass out through its posterior surface into the less dense medium of the vitreous humour. For a lens has the power of refracting and causing the convergence of the rays of a cone of light, not only on their entrance from a rarer medium into its anterior convex surface, but also at their exit from its posterior convex surface into the rarer medium.

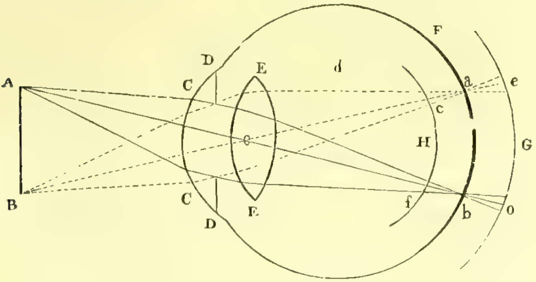


Fig. 379.—*Course of a ray of light.*

In this manner the rays of the cones of light issuing from the points A and B are again collected to points *a* and *b*; and, if the retina F be situated at *a* and *b*, perfect, though reversed, images of the points A and B will be formed upon it: but if the retina be not at *a* and *b*, but either before or behind that situation,—for instance, at H or G,—circular luminous spots *c* and *f*, or *e* and *o*, instead of points, will be seen; for at H the rays have not yet met, and at G they have already intersected each other, and are again diverging.

The retina must therefore be situated at the proper focal distance from the lens, otherwise a defined image will not be formed; or, in other words, the rays emitted by a given point of the object will not be collected into a corresponding point of focus upon the retina.

Defects in the Apparatus.

A. **Defects in the Refracting Media.**—Under this head we may consider the defects known as (1) Myopia, (2) Hypermetropia, (3) Astigmatism, (4) Spherical Aberration, (5) Chromatic Aberration.

The normal (emmetropic) eye is so adjusted that parallel rays are brought exactly to a focus on the retina without any effort of accommodation (1, fig. 380). Hence all objects except near ones (practically all objects more than twenty feet off) are seen without any effort of accommodation; in other words, the far-point of the normal eye is at an infinite distance. In viewing near objects we are conscious of an effort (the contraction of the ciliary muscle) by which the anterior surface of the lens is rendered more convex, and rays which would otherwise be focussed *behind* the retina are converged upon the retina (see dotted lines, 2, fig. 380).

1. **Myopia** (short-sight) (4, fig. 380).—This defect is due to an abnormal elongation of the eye-ball. The eye is usually larger than normal, and is always longer than normal; the lens is also probably too convex. The retina is too far from the lens, and consequently parallel rays are focussed in front of the retina, and, crossing, form little circles on the retina; thus the images of distant objects are blurred and indistinct. The eye is, as it were, permanently adjusted for a near-point. Rays from a point near the eye are exactly focussed in the retina. But those which issue from any object beyond a certain distance (*far-point*) cannot be distinctly focussed. This defect is corrected by *concave* glasses, which cause the rays entering the eye to diverge; hence they do

not come to a focus so soon. Such glasses of course are only needed to give a clear vision of distant objects. For near objects, except in extreme cases they are not required.

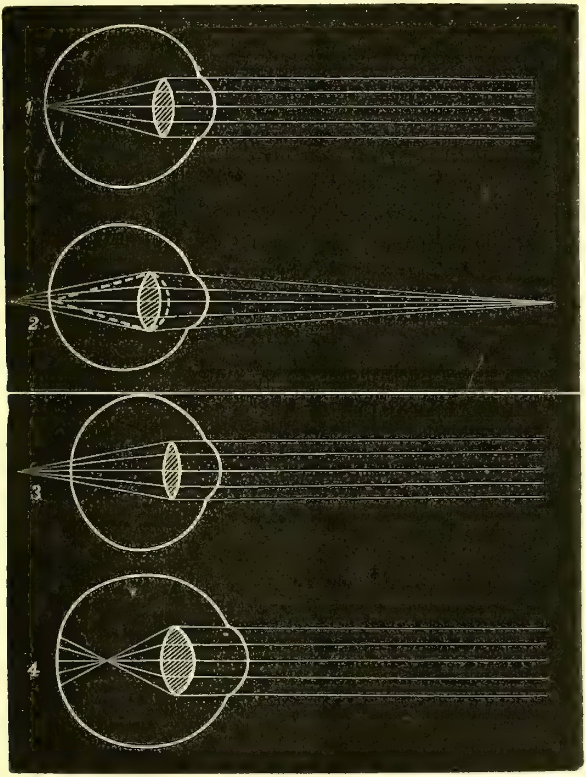


Fig. 380.—*Diagrams showing*—1, *normal* (*emmetropic*) *eye bringing parallel rays exactly to a focus on the retina*; 2, *normal eye adapted to a near point*; without accommodation the rays would be focussed behind the retina, but by increasing the curvature of the anterior surface of the lens (shown by a dotted line) the rays are focussed on the retina (as indicated by the meeting of the two dotted lines); 3, *hypermetropic* eye, in this case the axis of the eye is shorter, and the lens flatter, than normal; parallel rays are focussed behind the retina; 4, *myopic* eye; in this case the axis of the eye is abnormally long, and the lens too convex; parallel rays are focussed in front of the retina.

2. **Hypermetropia** (long-sight) (3, fig. 380).—This is the reverse defect. The eye is too short and the lens too flat. Parallel rays are focussed *behind* the retina: an effort of accommodation is required to focus even parallel rays on the retina; and when they are divergent, as in viewing a near object, the accommo-

dation is insufficient to focus them. Thus in well-marked cases distant objects require an effort of accommodation and near ones a very powerful effort. Thus the ciliary muscle is constantly acting. This defect is obviated by the use of *convex* glasses, which render the pencils of light more convergent. Such glasses are of course especially needed for near objects, as in reading, etc. They rest the eye by relieving the ciliary muscle from excessive work.

3. **Astigmatism.**—This defect, which was first discovered by Airy, is due to a greater curvature of the eye in one meridian than in others. The eye may be even myopic in one plane and hypermetropic in others. Thus vertical and horizontal lines crossing each other cannot both be focussed at once ; one set stand out clearly and the others are blurred and indistinct. This defect, which is present in a slight degree in all eyes, is generally seated in the cornea, but occasionally in the lens as well ; it may be corrected by the use of cylindrical glasses (*i.e.* curved only in one direction).

4. **Spherical Aberration.**—The rays of a cone of light from an object situated at the side of the field of vision do not meet all in the same point, owing to their unequal refraction ; for the refraction of the rays which pass through the circumference of a lens is greater than that of those traversing its central portion. This defect is known as *spherical aberration*, and in the camera, telescope, microscope, and other optical instruments, it is remedied by the interposition of a screen with a circular aperture in the path of the rays of light, cutting off all the marginal rays and only allowing the passage of those near the centre. Such correction is effected in the eye by the iris, which forms an annular diaphragm to cover the circumference of the lens, and to prevent the rays from passing through any part of the lens but its centre which corresponds to the pupil. The posterior surface of the iris is coated with pigment, to prevent the passage of rays of light through its substance. The image of an object will be most defined and distinct when the pupil is narrow, the object at the proper distance for vision, and the light abundant ; so that, while a sufficient number of rays are admitted, the narrowness of the pupil may prevent the production of indistinctness of the image by *spherical aberration*. But even the image formed by the rays passing through the circumference of the lens, when the pupil is

much dilated, as in the dark, or in a feeble light, may, under certain circumstances, be well defined.

Distinctness of vision is further secured by the outer surface of the retina as well as the posterior surface of the iris and the ciliary processes, being coated with black pigment, which absorbs any rays of light that may be reflected within the eye, and prevents their being thrown again upon the retina so as to interfere with the images there formed. The pigment of the retina is especially important in this respect; for with the exception of its outer layer the retina is very transparent, and if the surface behind it were not of a dark colour, but capable of reflecting the light, the luminous rays which had already acted on the retina would be reflected again through it, and would fall upon other parts of the same membrane, producing both dazzling from excessive light, and indistinctness of the images.

5. **Chromatic Aberration.**—In the passage of light through an ordinary convex lens, decomposition of each ray into its elementary coloured parts commonly ensues, and a coloured margin appears around the image, owing to the unequal refraction which the elementary colours undergo. In optical instruments this, which is termed *chromatic aberration*, is corrected by the use of two or more lenses, differing in shape and density, the second of which continues or increases the refraction of the rays produced by the first, but by recombining the individual parts of each ray into its original white light, corrects any chromatic aberration which may have resulted from the first. It is probable that the unequal refractive power of the transparent media in front of the retina may be the means by which the eye is enabled to guard against the effect of chromatic aberration. The human eye is achromatic, however, only so long as the image is received at its focal distance upon the retina, or so long as the eye adapts itself to the different distances of sight. If either of these conditions be interfered with, a more or less distinct appearance of colours is produced.

An ordinary ray of white light in passing through a prism, is refracted, *i.e.*, bent out of its course, but the different coloured rays which go to make up white light are refracted in different degrees, and therefore appear as coloured bands fading off into each other: thus a coloured band known as the "spectrum" is produced the colours of which are arranged as follows,—red, orange, yellow, green, blue, indigo, violet; of these the red ray is the least, and the violet the most refracted. Hence, as Helmholtz has shown, a small white object cannot be accurately focussed on the retina, for if we focus for the red rays, the violet are out of focus, and *vice versâ:* such objects, if not exactly focussed, are often seen surrounded by a pale yellowish or bluish fringe.

For similar reasons a red surface looks nearer than a blue one at an equal distance, because, the red rays being less refrangible, a stronger effort of accommodation is necessary to focus them, and the eye is adjusted as if for a nearer object, and therefore the red surface appears nearer.

From the insufficient adjustment of the image of a small white object, it appears surrounded by a sort of halo or fringe. This phenomenon is termed *Irradiation.* It is from this reason that a white square on a black ground appears larger than a black square of the same size on white ground.

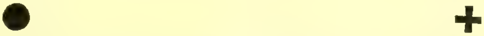
As an optical instrument, *the eye is superior to the camera* in the following, among many other particulars, which may be enumerated in detail. 1. The correctness of images even in a large field of view. 2. The simplicity and efficiency of the means by which chromatic aberration is avoided. 3. The perfect efficiency of its adaptation to different distances. In the photographic camera, it is well known that only a comparatively small object can be accurately focussed. In the photograph of a large object near at hand, the upper and lower limits are always more or less hazy, and vertical lines appear curved. This is due to the fact that the image produced by a convex lens is really slightly curved and can only be received without distortion on a slightly curved concave screen, hence the distortion on a *flat* surface of ground glass. It is different with the eye, since it possesses a concave background, upon which the field of vision is depicted, and with which the curved form of the image coincides exactly. Thus, the defect of the camera obscura is entirely avoided; for the eye is able to embrace a large field of vision, the margins of which are depicted distinctly and without distortion. If the retina had a plane surface like the ground glass plate in a camera, it must necessarily be much larger than is really the case if we were to see as much; moreover, the central portion of the field of vision alone would give a good clear picture. (Bernstein.)

B. **Defective Accommodation—Presbyopia.**—This condition is due to the gradual loss of the power of accommodation which is part of the general decay of old age. In consequence the patient would be obliged in reading to hold his book further and further away in order to focus the letters, till at last the letters are held too far for distinct vision. The defect is remedied by weak convex glasses, which are very commonly worn by old people. It is due chiefly to the gradual increase in density of the lens, which is unable to swell out and become convex when near objects are looked at, and also to a weakening of the ciliary muscle, and a general loss of elasticity in the parts concerned in the mechanism.

Visual Sensations.

Excitation of the Retina.—Light is the normal agent in the excitation of the retina, the only layer of which capable of reacting to the stimulus being the rods and cones. The proofs of this statement may be summed up thus :—

(1.) The point of entrance of the optic nerve into the retina, where the rods and cones are absent, is insensitive to light and is called the *blind spot*. The phenomenon itself is very readily demonstrated. If we direct one eye, the other being closed, upon a point at such a distance to the side of any object, that the image of the latter must fall upon the retina at the point of entrance of the optic nerve, this image is lost either instantaneously, or very soon. If, for example, we close the left eye, and direct the axis of the right eye steadily towards the circular spot here represented, while the page is held at a distance of about six inches from the eye, both dot and cross are visible. On gradually increasing the distance between the eye and the object, by removing the book farther and farther from the face, and still keeping the right eye steadily on the dot, it will be found that suddenly the cross disappears from view, while on removing the book still farther, it suddenly comes in sight again. The cause of this phenomenon is simply that the portion of retina which is occupied by the entrance of the optic nerve, is quite blind ; and therefore that when it alone occupies the field of vision, objects cease to be visible. (2.) In the fovea centralis and macula lutea, which contain rods and cones but no optic nerve-fibres, light produces the greatest effect. In the latter, cones occur in larger numbers, and in the former cones without rods are found, whereas in the rest of the retina which is



not so sensitive to light, there are fewer cones than rods. We may conclude, therefore, that cones are even more important to vision than rods. (3.) If a small lighted candle be moved to and fro at the side of and close to one eye in a dark room while the eyes look steadily forward into the darkness, a remarkable branching figure (*Purkinje's figures*) is seen floating before the eye, consisting of dark lines on a reddish ground. As the candle moves, the figure moves in the opposite direction, and from its whole appearance there can be no doubt that it is a reversed picture of the retinal vessels projected before the eye. The two large branching arteries passing up and down from the optic disc are clearly visible together with their minutest branches. A little to one side of the disc, in a part free from vessels, is seen the yellow spot in the form of a slight depression. This remarkable appearance is doubtless due to shadows of the retinal vessels cast by the candle. The branches of these vessels are chiefly distributed in the nerve-fibre and ganglionic layers; and since the light of the candle falls on the retinal vessels from in front, the shadow is cast behind them, and hence those elements of the retina which perceive the shadows must also lie behind the vessels. Here, then, we have a clear proof that the light-perceiving elements of the retina are not the fibres of the optic nerve forming the innermost layer of the retina, but the external layers of the retina, almost certainly the rods and cones, which indeed appear to be the special terminations of the optic nerve-fibres.

Duration of Visual Sensations.—The *duration* of the sensation produced by a luminous impression on the retina is always greater than that of the impression which produces it. However brief the luminous impression, the effect on the retina always lasts for about one-eighth of a second. Thus, supposing an object in motion, say a horse, to be revealed on a dark night by a flash of lightning. The object would be seen apparently for an eighth of a second, but it would not appear in motion; because, although the image remained on the retina for this time, it was really revealed for such an extremely short period (a flash of lightning being almost instantaneous) that no appreciable movement on the part of the object could have taken place in the period during which it was revealed to the retina of the observer. And the same fact is proved in a reverse way. The spokes of a rapidly revolving wheel are not seen as distinct objects, because at every point of the field of vision over which the revolving spokes pass, a given impression has not faded before another comes to replace it. Thus every part of the interior of the wheel appears occupied.

The duration of the *after-sensation*, produced by an object, is greater in a direct ratio with the duration of the impression which caused it. Hence the image of a bright object, as of the panes of a window through which the light is shining, may be perceived in the retina for a considerable period, if we have previously kept our eyes fixed for some time on it. But the image in this case is *negative.* If, however, after shutting the eyes for some time, we open them and look at an object for an instant, and again close them, the after-image is *positive.*

Intensity of Visual Sensations.—It is quite evident that the more luminous a body the more intense is the sensation it produces. But the intensity of the sensation is not *directly* proportional to the intensity of the luminosity of the object. It is necessary for light to have a certain intensity before it can excite the retina, but it is impossible to fix an arbitrary limit to the power of excitability. As in other sensations, so also in visual sensations, a stimulus may be too feeble to produce a sensation. If it be increased in amount sufficiently it begins to produce an effect which is increased on the increase of the stimulation; this increase in the effect is not *directly* proportional to the increase in the excitation, but, according to *Fechner's law*, "as the logarithm of the stimulus," *i.e.,* in each sensation, there is a constant ratio between the increase in the stimulus and the increase in the sensation, this constant ratio for each sensation expresses the least perceptible increase in the sensation or minimal increment of excitation.

This law, which is true only within certain limits, may be best understood by an example. When the retina has been stimulated by the light of one candle, the light of two candles will produce a difference in sensation which can be distinctly felt. If, however, the first stimulus had been that of an electric light, the addition of the light of a candle would make no difference in the sensation. So, generally, for an additional stimulus to be felt, it may be proportionately small if the original stimulus have been small, and must be greater if the original stimulus have been great. The stimulus increases as the ordinary numbers, while the sensation increases as the logarithm.

The Ophthalmoscope.—Part of the light which enters the eye is absorbed, and produces some change in the retina, of which we shall treat further on ; the rest is reflected.

Every one is perfectly familiar with the fact, that it is quite impossible to see the *fundus* or back of another person's eye by simply looking into it. The interior of the eye forms a perfectly black background to the pupil. The same remark applies to an ordinary photographic camera, and may be illustrated by the difficulty we experience in seeing into a room from the street through the window, unless the room be lighted within. In the case of the eye this fact is partly due to the feebleness of the light reflected from the retina, most of it being absorbed by the choroid, as mentioned above ; but far more to the fact that every such ray is reflected straight back to the source of light (*e.g.*, candle), and cannot, therefore, be seen by the unaided eye without intercepting the incident light from the candle, as well as the reflected rays from the retina. This difficulty has been surmounted by the ingenious device of Helmholtz, now so extensively used, termed the *ophthalmoscope.* As at present used, it consists of a small slightly concave mirror, by which light is reflected from a candle into the eye. The observer looks through a hole in the mirror, and can thus explore the illuminated fundus ; the entrance of the optic nerve and the retinal vessels being plainly visible.

Visual Purple.—The method by which a ray of light is able to stimulate the endings of the optic nerve in the retina in such a manner that a visual sensation is perceived by the cerebrum is not yet understood. It is supposed that the change effected by the agency of the light which falls upon the retina is in fact a chemical alteration in the protoplasm, and that this change stimulates the optic nerve-endings. The discovery of a certain temporary reddish-purple pigmentation of the outer limbs of the retinal rods in certain animals (*e.g.* frogs) which have been killed in the dark, forming the so-called *visual purple*, appeared likely to offer some explanation of the matter, especially as it was also found that the pigmentation disappeared when the animal was exposed to light, and re-appeared when the light was removed, and also that it underwent distinct changes of colour when other than white light was used. The visual purple cannot however be absolutely essential to the due production of visual sensations, as it is absent from the retinal cones, and from the macula lutea and fovea centralis of the human retina, and does not appear to exist at all in the retinas of some animals, *e.g.*, bat, dove, and hen, which are, nevertheless, possessed of good vision.

If the operation be performed quickly enough, the image of an object may be fixed in the pigment on the retina by soaking the retina of an animal, which has been killed in the dark, in alum solution.

Electrical Currents.—According to the careful researches of Dewar and McKendrick, and of Holmgren, it appears that the stimulus of light is able to produce a variation of the natural electrical current of the retina. The current is at first increased and then diminished. McKendrick believes that this is the electrical expression of those chemical changes in the retina of which we have already spoken.

Visual Perceptions and Judgments.

Reversion of the Image.—The direction given to the rays by their refraction is regulated by that of the central ray, or axis of the cone, towards which the rays are bent. The image of any point of an object is, therefore, as a rule (the exceptions to which need not here be stated), always formed in a line identical with the axis of the cone of light, as in the line of B *a*, or A *b* (fig. 381), so that the spot where the image of any point will be formed upon the retina may be determined by prolonging the central ray of the cone of light, or that ray which traverses the centre of the pupil. Thus A *b* is the axis or central ray of the cone of light issuing from A; B *a* the central ray of the cone of light issuing from B; the image of A is formed at *b*, the image of B at *a*, in the

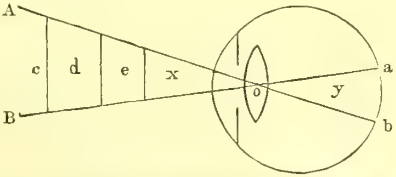


Fig. 381.—*Diagram of the formation of the image on the retina.*

inverted position; therefore what in the object was above is in the image below, and *vice versa*,—the right hand part of the object is in the image to the left, the left-hand to the right. If an opening be made in an eye at its superior surface, so that the retina can be seen through the vitreous humour, this reversed image of any bright object, such as the windows of the room, may be perceived at the bottom of the eye. Or still better, if the eye of any albino animal, such as a white rabbit, in which the coats, from the absence of pigment, are transparent, is dissected clean, and held with the cornea towards the window, a very distinct image of the window completely inverted is seen depicted on the posterior translucent wall of the eye. Volkmann has also shown that a similar experiment may be successfully performed in a living person possessed of large prominent eyes, and an unusually transparent sclerotic.

An image formed at any point on the retina is referred to a point outside the eye, lying on a straight line drawn from the point on the retina outwards through the centre of the pupil. Thus an image on the left side of the retina is referred by the mind to an object on the right side of the eye, and *vice versâ*. Thus all images on the retina are mentally, as it were, projected in front of the eye, and the objects are seen *erect* though the image on the retina is *reversed*. Much needless confusion and difficulty have been raised on this subject for want of remembering that when we are said to *see* an object, the mind is merely conscious of the picture on the retina, and when it refers it to the external object, or "projects" it outside the eye, it *necessarily* reverses it and sees the object as erect, though the retinal image is inverted. This is further corroborated by the sense of touch. Thus an object whose picture falls on the left half of the retina is reached by the right hand, and hence is said to lie to the *right*. Or, again, an object whose image is formed on the upper part of the retina is readily touched by the feet, and is therefore said to be in the *lower* part of the field, and so on.

Hence it is, also, that no discordance arises between the sensations of inverted vision and those of touch, which perceives everything in its erect position; for the images of all objects, even of our own limbs, in the retina, are equally inverted, and therefore maintain the same relative position.

Even the image of our hand, while used in touch, is seen inverted. The position in which we see objects, we call, therefore, the erect position. A mere lateral inversion of our body in a mirror, where the right hand occupies the left of the image, is indeed scarcely remarked: and there is but little discordance between the sensations acquired by touch in regulating our movements by the image in the mirror, and those of sight, as, for example, in tying a knot in the cravat. There is some want of harmony here, on account of the inversion being only lateral, and not complete in all directions.

The perception of the erect position of objects appears, therefore, to be the result of an act of the mind. And this leads us to a consideration of the several other properties of the retina, and of the co-operation of the mind in the several other parts of the act of vision. To these belong not merely the act of sensation itself and the perception of the changes produced in the retina, as light and colours, but also the conversion of the mere images depicted in the retina into ideas of an extended field of vision, of proximity and distance, of the form and size of objects, of the reciprocal influence of different parts of the retina upon each other, the simultaneous action of the two eyes, and some other phenomena.

Field of Vision.—The actual size of the field of vision depends on the extent of the retina, for only so many images can be seen at any one time as can occupy the retina at the same time; and thus considered, the retina, of which the affections are perceived by the mind, is itself the field of vision. But to the mind of the individual the size of the field of vision has no determinate limits; sometimes it appears very small, at another time very large; for the mind has the power of projecting images on the retina towards the exterior. Hence the mental field of vision is very small when the sphere of the action of the mind is limited to impediments near the eye: on the contrary, it is very extensive when the projection of the images on the retina towards the exterior, by the influence of the mind, is not impeded. It is very small when we look into a hollow body of small capacity held before the eyes; large when we look out upon the landscape through a small opening; more extensive when we look at the landscape through a window; and most so when our view is not confined by any near object. In all these cases the idea which we receive of the size of the field of vision is very different, although its absolute size is in all the same, being dependent on the extent of the retina. Hence it follows, that the mind is constantly co-operating in the acts of vision, so that at last it becomes difficult to say what belongs to mere sensation, and what to the influence of the mind. By a mental operation of this kind, we obtain a correct idea of the size of individual objects, as well as of the extent of the field of vision. To illustrate this, it will be well to refer to fig. 382.

The angle x, included between the decussating central rays of two cones of light issuing from different points of an object, is called the optical angle—*angulus opticus seu visorius.* This angle becomes larger, the greater the distance between the points A and B; and since the angles x and y are equal, the distance between the points a and b in the image on the retina increases as the angle becomes larger. Objects at different distances from the eye, but having the same optical angle x—for example, the objects, c, d, and e,—must also throw images of equal size upon the retina; and, if they occupy the same angle of the field of vision, their image must occupy the same spot in the retina.

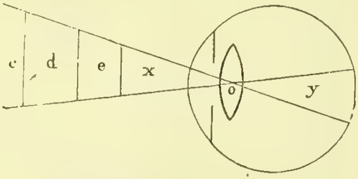


Fig. 382.—*Diagram of the optical angle.*

Nevertheless, these images appear to the mind to be of very unequal size when the ideas of distance and proximity come into play; for, from the image $a\ b$, the mind forms the conception of a visual space extending to e, d, or c, and of an object of the size which that represented by the image on the retina appears to have when viewed close to the eye, or under the most usual circumstances.

Estimation of Size.—Our estimate of the size of various objects is based partly on the visual angle under which they are seen, but much more on the estimate we form of their distance. Thus a lofty mountain many miles off may be seen under the same visual angle as a small hill near at hand, but we infer that the former is much the larger object because we know it is much further off than the hill. Our estimate of distance is often erroneous, and consequently the estimate of size also. Thus persons seen walking on the top of a small hill against a clear twilight sky appear unusually large, because we over-estimate their distance, and for similar reasons most objects in a fog appear immensely magnified. The same mental process gives rise to the idea of depth in the field of vision; this idea being fixed in our mind principally by the circumstance that, as we ourselves move forwards, different images in succession become depicted on our retina, so that we seem to pass between these images, which to the mind is the same thing as passing between the objects themselves.

The action of the sense of vision in relation to external objects is, therefore, quite different from that of the sense of touch. The objects of the latter sense are immediately present to it; and our own body, with which they come into contact, is the measure of their size. The part of a table touched by the hand appears as large as the part of the hand receiving an impression from it, for a part of our body in which a sensation is excited, is here the measure by which we judge of the magnitude of the object. In the sense of vision, on the contrary, the images of objects are mere fractions of the objects themselves realised upon the retina, the extent of which remains constantly the same. But the imagination, which analyses the sensations of vision, invests the images of objects, together with the whole field of vision in the retina, with very varying dimensions; the relative size of the image in proportion to the whole field of vision, or of the affected parts of the retina to the whole retina, alone remaining unaltered.

Estimation of Direction.—The direction in which an object is seen, depends on the part of the retina which receives the image, and on the distance of this part from, and its relation to, the central point of the retina. Thus, objects of which the images fall upon the same parts of the retina lie in the same visual direction; and when, by the action of the mind, the images or affections of the retina are projected into the exterior world, the relation of the images to each other remains the same.

Estimation of Form.—The estimation of the *form of bodies* by sight is the result partly of the mere sensation, and partly of the association of ideas. Since the form of the images perceived by the retina depends wholly on the outline of the part of the retina affected, the sensation alone is adequate to the distinction of only superficial forms of each other, as of a square from a circle. But the idea of a solid body as a sphere, or a body of three or more dimensions, *e.g.*, a cube, can only be attained by the action of the mind constructing it from the different superficial images seen in different positions of the eye with regard to the object, and, as shown by Wheatstone and illustrated in the *stereoscope*, from two different perspective projections of the body being presented simultaneously to the mind by the two eyes. Hence, when, in adult age, sight is suddenly restored to persons blind from infancy, all objects in the field of vision appear at first as if painted flat on one surface; and no idea of solidity is formed until after long exercise of the sense of vision combined with that of touch.

The *clearness* with which an object is perceived irrespective of accommodation, would appear to depend largely on the number of rods and cones which its retinal image covers. Hence the nearer an object is to the eye (within moderate limits) the more clearly are all its details seen. Moreover, if we want carefully to examine any object, we always direct the eyes straight to it, so that its image shall fall on the yellow spot where an image of a given area will cover a larger number of cones than anywhere else in the retina. It has been found that the images of two points must be at least $\frac{1}{12000}$ in. apart on the yellow spot in order to be distinguished separately; if the images are nearer together, the points appear as one. The diameter of each cone in this part of the retina is about $\frac{1}{12000}$ in.

Estimation of Movement.—We judge of the *motion* of an object, partly from the motion of its image over the surface of the retina, and partly from the motion of our eyes following it. If the image upon the retina moves while our eyes and our body are at rest, we conclude that the object is changing its relative position with regard to ourselves. In such a case the movement of the object may be apparent only, as when we are standing upon a body which is in motion, such as a ship. If, on the other hand, the image does not move with regard to the retina, but remains fixed upon the same spot of that membrane, while our eyes follow the moving body, we judge of the motion of the object by the sensation of the muscles in action to move the eye. If the image moves over the surface of the retina while the muscles of the eye are acting at the same time in a manner corresponding to this motion, as in reading, we infer that the object is stationary, and we know that we are merely altering the relations of our eyes to the object. Sometimes the object appears to move when both object and eye are fixed, as in vertigo.

The mind can, by the faculty of *attention*, concentrate its activity more or less exclusively upon the sense of sight, hearing, and touch alternately. When exclusively occupied with the action of one sense, it is scarcely conscious of the sensations of the others. The mind, when deeply immersed in contemplations of another nature, is indifferent to the actions of the sense of sight, as of every other sense. We often, when deep in thought, have our eyes open and fixed, but see nothing, because of the stimulus of ordinary light being unable to excite the brain to perception, when otherwise engaged. The attention which is thus necessary for vision, is necessary also to analyse what the field of vision presents. The mind does not perceive all the objects presented by the field of vision at the same time with equal acuteness, but directs itself first to one and then to another. The sensation becomes more intense, according as the particular object is at the time the principal object of mental contemplation. Any compound mathematical figure produces a different impression according as the attention is directed exclusively to one or the other part of it. Thus in fig. 383, we may in succession have a vivid perception of the whole, or of distinct parts only; of the six triangles near the outer circle, of the hexagon in the middle, or of the three large triangles. The more numerous and varied the parts of which a figure is composed, the more scope does it afford for the play of the attention. Hence it is that architectural ornaments have an enlivening effect on the sense of vision, since they afford constantly fresh subject for the action of the mind.

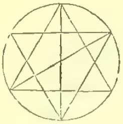


Fig. 383.

Colour Sensations.—If a ray of sunlight be allowed to pass through a prism, it is decomposed by its passage into rays of different colours, which are called the colours of the spectrum; they are red, orange, yellow, green, blue, indigo, and violet. The red rays are the least turned out of their course by the prism, and the violet the most, whilst the other colours occupy in order places between these two extremes. The differences in the colour of the rays, depend upon the number of vibrations producing each, the red rays being the least rapid and the violet the most. In addition to the coloured rays of the spectrum, there are others which are invisible, but which have definite properties, those to the left of the red, and less refrangible, being the calorific rays which act upon the thermometer, and those to the right of the violet which are called the actinic or chemical rays, which have a powerful chemical action. The rays which can be perceived by the brain as visual rays, *i.e.*, the coloured rays, must stimulate the retina in some special manner in order that coloured vision may result, and two chief explanations of the method of stimulation have been suggested. The one, originated by Young and elaborated by Helmholtz, holds that there are three primary colours, viz., red, green, and violet, and that in the retina are contained rods or cones which answer to each of these primary colours, whereas the innumerable intermediate shades of colour are produced by stimulation of the three primary colour terminals in different degrees; the sensation of white being produced when the three elements are equally excited. Thus if the retina be stimulated by rays of certain wave length, at the red end of the spectrum, the terminals of the other colours green and violet, are hardly stimulated at all, but the red terminals being strongly stimulated, the resulting sensation is red. The orange rays excite the red terminals considerably, the green rather more, and the violet slightly, the resulting sensation being that of orange, and so on.

The second theory of colour (Hering's) supposes that there are six primary colour sensations, of three pair of antagonistic or complemental colours, black and white, red and green, and yellow and blue, and that these are produced by the changes either of disintegration or of assimilation taking place in certain substances, somewhat it may be supposed of the nature of the visual purple, which (the theory supposes to) exist in the retina. Each of the substances corresponding to a pair of colours, being capable of undergoing two changes, one of construction and the other of disintegration, with the result of producing one or other colour. For instance, in the white-black substance, when disintegration is in excess of construction or assimilation, the sensation is white, and when assimilation is in excess of disintegration the reverse is the case; and similarly with the red-green substance, and with the yellow-blue substance. When the repair and disintegration are equal with the first substance, the visual sensation is grey; but in the other pairs when this is the case, no sensation occurs. The rays of the spectrum to the left produce changes in the red-green substance only, with a resulting sensation of red, whilst the (orange) rays further to the right affect both the red-green and the yellow-blue substances; blue rays cause constructive changes in the yellow-blue substance, but none in the red-green, and so on. These changes produced in the visual substances in the retina are perceived by the brain as sensations of colour.

The spectra left by the images of white or luminous objects, are ordinarily white or luminous; those left by dark objects are dark. Sometimes, however, the relation of the light and dark parts in the image may, under certain circumstances, be reversed in the spectrum; what was bright may be dark, and what was dark may appear light. This occurs whenever the eye, which is the seat of the spectrum of a luminous object, is not closed, but fixed upon another bright or white surface, as a white wall, or a sheet of white paper. Hence the spectrum of the sun, which, while light is excluded from the eye is luminous, appears black or grey when the eye is directed upon a white surface. The explanation of this is, that the part of the retina which has received the luminous image remains for a certain period afterwards in an exhausted or less sensitive state, while that which has received a dark image is in an unexhausted, and therefore much more excitable condition.

The ocular spectra which remain after the impression of coloured objects upon the retina are always coloured; and their colour is not that of the object, or of the image produced directly by the object, but the opposite, or *complemental* colour. The spectrum of a red object is, therefore, green; that of a green object, red; that of violet, yellow; that of yellow, violet, and so on. The reason of this is obvious. The part of the retina which receives, say, a red image, is wearied by that particular colour, but remains sensitive to the other rays which with red make up white light; and, therefore, these by themselves reflected from a white object produce a green hue. If, on the other hand, the first object looked at be green, the retina being tired of green rays, receives a red image when the eye is turned to a white object. And so with the other colours; the retina while fatigued by yellow rays will suppose an object to be violet, and *vice versâ;* the size and shape of the spectrum corresponding with the size and shape of the original object looked at. The colours which thus reciprocally excite each other in the retina are those placed at opposite points of the circle in fig. 384. The peripheral parts of the retina have no perception of *red.* The area of the retina which is capable of receiving impressions of colour is slightly different for each colour.

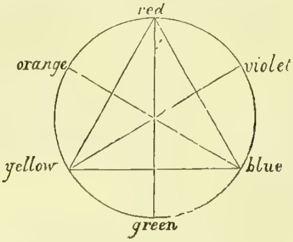


Fig. 384.—*Diagram of the various simple and compound colours of light, and those which are complemental of each other, i.e.*, which, when mixed, produce a neutral grey tint. The three simple colours, red, yellow, and blue, are placed at the angles of an equilateral triangle; which are connected together by means of a circle; the mixed colours, green, orange, and violet, are placed intermediate between the corresponding simple or homogeneous colours; and the complemental colours, of which the pigments, when mixed, would constitute a grey, and of which the prismatic spectra would together produce a white light, will be found to be placed in each case opposite to each other, but connected by a line passing through the centre of the circle. The figure is also useful in showing the further shades of colour which are complementary of each other. If the circle be supposed to contain every transition of colour between the six marked down, those which, when united, yield a white or grey colour, will always be found directly opposite to each other; thus, for example, the intermediate tint between orange and red is complemental of the middle tint between green and blue.

Colour Blindness or Daltonism.—*Daltonism* or colour-blindness is a by no means uncommon visual defect. One of the commonest forms is the inability to distinguish between red and green. The simplest explanation of such a condition is, that the elements of the retina which receive the impression of red, etc., are absent, or very imperfectly developed, or, according to the other theory, that the red-green substance is absent from the retina. Other varieties of colour blindness in which the other colour-perceiving elements are absent have been shown to exist occasionally.

Of the Reciprocal Action of Different Parts of the Retina on each other.

Although each elementary part of the retina represents a distinct portion of the field of vision, yet the different elementary parts, or sensitive points of that membrane, have a certain influence on each other; the particular condition of one influencing that of another, so that the image perceived by one part is modified by the image depicted in the other. The phenomena which result from this relation between the different parts of the retina, may be arranged in two classes; the one including those where the condition existing in the greater extent of the retina is imparted to the remainder of that membrane; the other, consisting of those in which the condition of the larger portion of the retina excites, in the less extensive portion, the opposite condition.

1. When two opposite impressions occur in contiguous parts of an image on the retina, the one impression is, under certain circumstances, modified by the other. If the impressions occupy each one-half of the image, this does not take place; for in that case their actions are equally balanced. But if one of the impressions occupies only a small part of the retina, and the other the greater part of its surface, the latter may, if long continued, extend its influence over the whole retina, so that the opposite less extensive impression is no longer perceived, and its place becomes occupied by the same sensation as the rest of the field of vision. Thus, if we fix the eye for some time upon a strip of coloured paper lying upon a white surface, the image of the coloured object, especially when it falls on the lateral parts of the retina, will gradually disappear, and the white surface be seen in its place.

2. In the second class of phenomena, the affection of one part of the retina influences that of another part, not in such a manner as to obliterate it, but so as to cause it to become the contrast or opposite of itself. Thus a grey spot upon a white ground appears darker than the same tint of grey would do if it alone occupied the whole field of vision, and a shadow is always rendered deeper when the light which gives rise to it becomes more intense, owing to the greater contrast.

The former phenomena ensue gradually, and only after the images have been long fixed on the retina; the latter are instantaneous in their production, and are permanent.

In the same way, also, colours may be produced by contrast. Thus, a very small dull grey strip of paper, lying upon an extensive surface of any bright colour, does not appear grey, but has a faint tint of the colour which is the complement of that of the surrounding surface. A strip of grey paper upon a green field, for example, often appears to have a tint of red, and when lying upon a red surface, a greenish tint; it has an orange-coloured tint upon a bright blue surface, and a bluish tint upon an orange-coloured surface; a yellowish colour upon a bright violet, and a violet tint upon a bright yellow surface. The colour excited thus, as a contrast to the exciting colour, being wholly independent of any rays of the corresponding colour acting from without upon the retina, must arise as an opposite or antagonistic condition of that membrane; and the opposite conditions of which the retina thus becomes the subject would seem to balance each other by their reciprocal reaction. A necessary condition for the production of the contrasted colours is, that the part of the retina in which the new colour is to be excited, shall be in a state of comparative repose; hence the small object itself must be grey. A second condition is, that the colour of the surrounding surface shall be very bright, that is, it shall contain much white light.

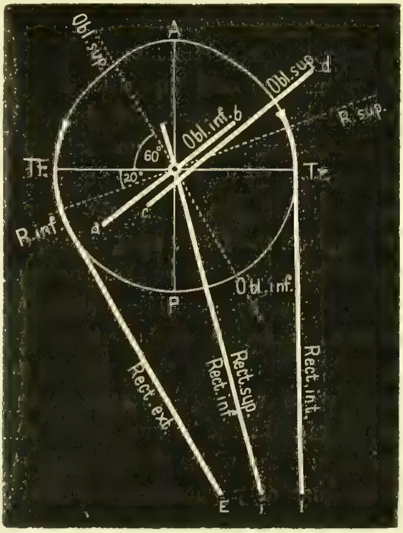


Fig. 385.—*Diagram of the axes of rotation to the eye.* The thin lines indicate axes of rotation, the thick the position of muscular attachment. (Modified from Fick.)

Movements of the Eye.—The eyeball possesses movement around three axes indicated in fig. 385, viz., an antero-posterior, a vertical, and a transverse, passing through a centre of rotation a little behind the centre of the optic axis. The movements are accomplished by pairs of muscles.

Movements.	*By what muscles accomplished.*
Inwards	Internal rectus.
Outwards	External rectus.
Upwards	Superior rectus. Inferior oblique.
Downwards	Inferior rectus. Superior oblique.
Inwards and upwards	Internal and superior rectus. Inferior oblique.
Inwards and downwards	Internal and inferior rectus. Superior oblique.
Outwards and upwards	External and superior rectus. Inferior oblique.
Outwards and downwards	External and inferior rectus. Superior oblique.

Of the Simultaneous Action of the two Eyes.

Although the sense of sight is exercised by two organs, yet the impression of an object conveyed to the mind is single. Various theories have been advanced to account for this phenomenon. By Gall it was supposed that we do not really employ both eyes simultaneously in vision, but always see with only one at a time. This especial employment of one eye in vision certainly occurs in persons whose eyes are of very unequal focal distance, but in the majority of individuals both eyes are simultaneously in action, in the perception of the same object; this is shown by the double images seen under certain conditions. If two fingers be held up before the eyes, one in front of the other, and vision be directed to the more distant, so that it is seen singly, the nearer will appear double; while, if the nearer one be regarded, the most distant will be seen double; and one of the double images in each case will be found to belong to one eye, the other to the other eye.

Diplopia.—Single vision results only when certain parts of the two retinæ are affected simultaneously; if different parts of the retinæ receive the image of the object, it is seen double. This may be readily illustrated as follows:—The eyes are fixed upon some near object, and one of them is pressed by the thumb so as to be turned slightly in or out; two images of the object (*Diplopia* or Double Vision) are at once perceived, just as is frequently the case in persons who squint. This diplopia is due to the fact that the images of the object do not fall on corresponding points in the two retinæ.

The parts of the retinæ in the two eyes which thus correspond to each other in the property of referring the images which affect them simultaneously to the same spot in the field of vision, are, in man, just those parts which would correspond to each other, if one retina were placed exactly in front of, and over the other (as in fig. 386, c). Thus, the outer lateral portion of one eye corresponds to, or, to use a better term, is identical with the inner portion of the other eye; or *a* of the eye A (fig. 386), with *a′* of the eye B. The upper part of one retina is also identical with the upper part of the other; and the lower parts of the two eyes are identical with each other.

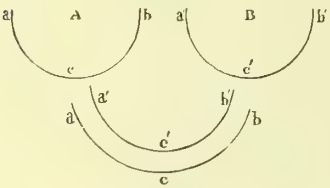


Fig. 386.

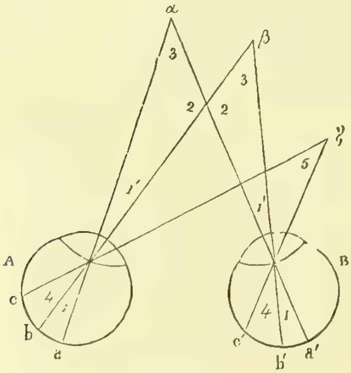


Fig. 387.

This is proved by a simple experiment. Pressure upon any part of the ball of the eye, so as to affect the retina, produces a luminous circle, seen at the opposite side of the field of vision to that on which the pressure is made. If, now, in a dark room, we press with the finger at the upper part of one eye, and at the lower part of the other, two luminous circles are seen, one above the other: so, also, two figures are seen when pressure is made simultaneously on the two outer or the two inner sides of both eyes. It is certain, therefore, that neither the upper part of one retina and the lower part of the other are identical, nor the outer lateral parts of the two retinæ, nor their inner lateral portions. But if pressure be made with the fingers upon both eyes simultaneously at their lower part, one luminous ring is seen at the middle of the upper part of the field of vision; if the pressure be applied to the upper part of both eyes a single luminous circle is seen in the middle of the field of vision below. So, also, if we press upon the outer side *a* of the eye A, and upon the inner side *a′* of the eye B, a single spectrum is produced, and is apparent at the extreme right of the field of vision; if upon the point *b* of one eye, and the point *b′* of the other, a single spectrum is seen to the extreme left.

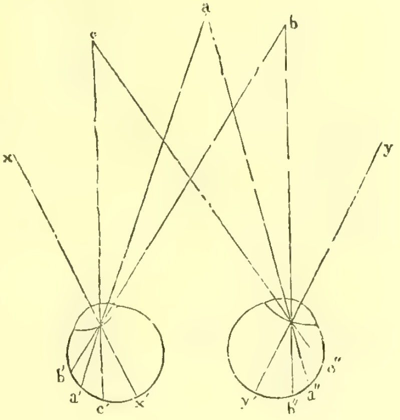


Fig. 388.

The spheres of the two retinæ may, therefore, be regarded as lying one over the other, as in C, fig. 386; so that the left portion of one eye lies over the identical left portion of the other eye, the right portion of one eye over the identical right portion of the other eye; and with the upper and lower portions of the two eyes, *a* lies over *a′*, *b* over *b′*, and *c* over *c′*. The points of the one retina intermediate between *a* and *c* are again identical with the corresponding points of the other retina between *a′* and *c′*; those between *b* and *c* of the one retina, with those between *b′* and *c′* of the other. If the axes of the eyes, A and B (fig, 388), be so directed that they meet at *a*, an object at *a* will be seen singly, for the point *a* of the one retina, and *a′* of the other, are identical. So, also, if the object *β* be so situated that its image falls in both eyes at the same distance from the central point of the retina,—namely, at *b* in the one eye, and at *b'* in the other,—β will be seen single, for it affects identical parts of the two retinæ. The same will apply to the object γ.

In quadrupeds, the relation between the identical and non-identical parts of the retina cannot be the same as in man; for the axes of their eyes generally diverge, and can never be made to meet in one point of an object. When an animal regards an object situated directly in front of it, the image of the object must fall, in both eyes, on the outer portion of the retinæ. Thus, the image of the object *a* (fig. 389) will fall at *a'* in one, and at *a''* in the other: and these points *a'* and *a''* must be identical. So, also, for distinct and single vision of objects, *b* or *c*, the points *b'* and *b''* or *c' c''*, in the two retinæ, on which the images of these objects fall, must be identical. All points of the retina in each eye which receive rays of light from lateral objects only, can have no corresponding identical points in the retina of the other eye; for otherwise two objects, one situated to the right and the other to the left, would appear to lie in the same spot of the field of vision. It is probable, therefore, that there are in the eyes of animals, parts of the retinæ which are identical, and parts which are not identical, *i.e.*, parts in one which have no corresponding parts in the other eye. And the relation of the two retinæ to each other in the field of vision may be represented as in fig. .

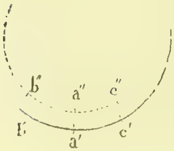


Fig. 389.

Binocular Vision.—The cause of the impressions on the identical points of the two retinæ giving rise to but one sensation, and the perception of a single image, must either lie in the structural organisation of the deeper or cerebral portion of the visual apparatus, or be the result of a mental operation; for in no other case is it the property of the corresponding nerves of the two sides of the body to refer their sensations as one to one spot.

Many attempts have been made to explain this remarkable relation between the eyes, by referring it to anatomical relation between the optic nerves. The circumstance of the inner portion of the fibres of the two optic nerves decussating at the commissure, and passing to the eye of the opposite side, while the outer portion of the fibres continue their course to the eye of the same side, so that the left side of both retinæ is formed from one root of the nerves, and the right side of both retinæ from the outer root, naturally led to an attempt to explain the phenomenon by this distribution of the fibres of the nerves.

And this explanation is favoured by cases in which the entire of one side of the retina, as far as the central point in both eyes, sometimes becomes insensible. But Müller shows the inadequateness of this theory to explain the phenomenon, unless it be supposed that each fibre in each cerebral portion of the optic nerves divides in the optic commissure into two branches for the identical points of the two retinæ, as is shown in A, fig. 390. But there is no foundation for such supposition.

By another theory it is assumed that each optic nerve contains exactly the same number of fibres as the other, and that the corresponding fibres of the two nerves are united in the Sensorium (as in fig. 390, B). But in this theory no account is taken of the partial decussation of the fibres of the nerves in the optic commissure.

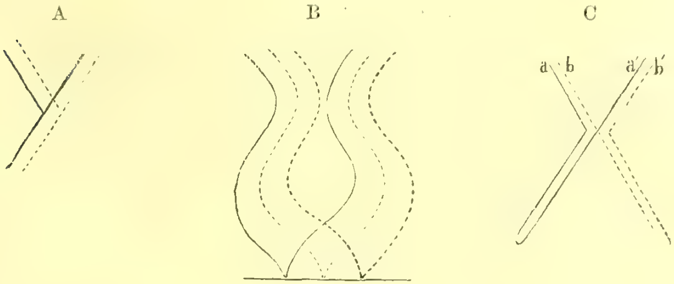


Fig. 390.

According to a third theory, the fibres *a* and *a'*, fig. 390, C, coming from identical points of the two retinæ, are in the optic commissure brought into one optic nerve, and in the brain either are united by a loop, or spring from the same point. The same disposition prevails in the case of the identical fibres *b* and *b'*. According to this theory, the left half of each retina would be represented in the left hemisphere of the brain, and the right half of each retina in the right hemisphere.

Another explanation is founded on the fact, that at the anterior part of the commissure of the optic nerve, certain fibres pass across from the distal portion of one nerve to the corresponding portion of the other nerves, as if they were commissural fibres forming a connection between the retinæ of the two eyes. It is supposed, indeed, that these fibres may connect the corresponding parts of the two retinæ, and may thus explain their unity of action; in the same way that corresponding parts of the cerebral hemispheres are believed to be connected together by the comissural fibres of the corpus callosum, and so enabled to exercise unity of function.

Judgment of Solidity.—On the whole, it is probable, that the power of forming a single idea of an object from a double impression conveyed by it to the eyes is the result of a mental act. This view is supported by the same facts as those employed by Wheatstone to show that this power is subservient to the purpose of obtaining a right perception of bodies raised in relief. When an object is placed so near the eyes that to view it the optic axes must converge, a different perspective projection of it is seen by each eye, these perspectives being more dissimilar as the convergence of the optic axes becomes greater. Thus, if any figure of three dimensions, an outline cube, for example, be held at a moderate distance before the eyes, and viewed with each eye successively while the head is kept perfectly steady, A (fig. 391) will be the picture presented to the right eye, and B that seen by the left eye. Wheatstone has shown that on this circumstance depends in a great measure our conviction of the solidity of an object, or of its projection in relief. If different perspective drawings of a solid body, one representing the image seen by the right eye, the other that seen by the left (for example, the drawing of a cube, A, B, fig. 391), be presented to corresponding parts of the two retinæ, as may be readily done by means of the stereoscope, the mind will perceive not merely a single representation of the object, but a body projecting in relief, the exact counterpart of that from which the drawings were made.

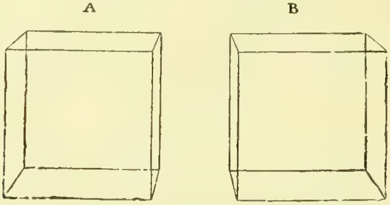


Fig. 391.

By transposing two stereoscopic pictures a reverse effect is produced: the elevated parts appear to be depressed, and *vice versâ.* An instrument contrived with this purpose is termed a *pseudoscope.* Viewed with this instrument a bust appears as a hollow mask, and as may readily be imagined the effect is most bewildering.

CHAPTER XX

GENERATION AND DEVELOPMENT.

The several organs and functions of the human body which have been considered in the previous chapters, have relation to the individual being. We have now to consider those organs and functions which are destined for the propagation of the species. These comprise the several provisions made for the formation, impregnation, and development of the ovum, from which the embryo or fœtus is produced and gradually perfected into a fully-formed human being.

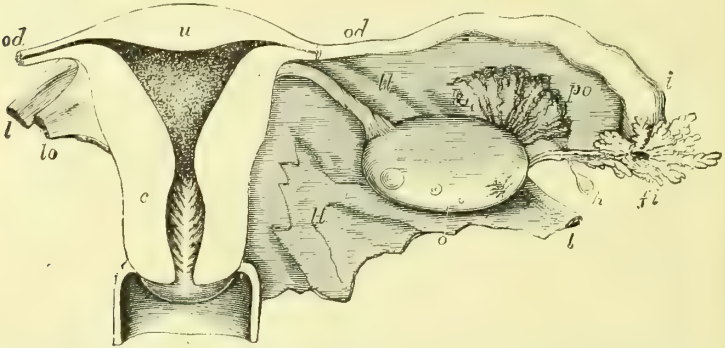


Fig. 392.—*Diagrammatic view of the uterus and its appendages, as seen from behind.* The uterus and upper part of the vagina have been laid open by removing the posterior wall; the Fallopian tube, round ligament, and ovarian ligament have been cut short, and the broad ligament removed on the left side; *u*, the upper part of the uterus; *c*, the cervix opposite the os internum; the triangular shape of the uterine cavity is shown, and the dilatation of the cervical cavity with the rugæ termed arbor vitæ; *v*, upper part of the vagina; *od*, Fallopian tube or oviduct; the narrow communication of its cavity with that of the cornu of the uterus on each side is seen; *l*, round ligament: *lo*, ligament of the ovary; *o*, ovary; *i*, wide outer part of the right Fallopian tube; *fi*, its fimbriated extremity; *po*, parovarium; *h*, one of the hydatids frequently found connected with the broad ligament. ½. (Allen Thomson.)

The organs in the two sexes concerned in effecting these objects are named the Generative organs, or Sexual apparatus.

Generative Organs of the Female.

The female organs of generation (fig. 392) consist of two *Ovaries*, whose function is the formation of ova; of a *Fallopian* *tube*, or oviduct, connected with each ovary, for the purpose of conducting the ovum from the ovary to the *Uterus* or cavity in which, if impregnated, it is retained until the embryo is fully developed, and fitted to maintain its existence independently of internal connection with the parent; and, lastly, of a canal, or *Vagina*, with its appendages, for the reception of the male generative organs in the act of copulation, and for the subsequent discharge of the fœtus.

Ovaries.—The *ovaries* are two oval compressed bodies, situated in the cavity of the pelvis, one on each side, enclosed in the folds of the broad ligament. Each ovary measures about an inch and a half in length, three-quarters of an inch in width, and nearly half an inch in thickness, and is attached to the uterus by a narrow fibrous cord (the ligament of the ovary), and, more slightly, to the Fallopian tubes by one of the fimbriæ into which the walls of the extremity of the tube expand.

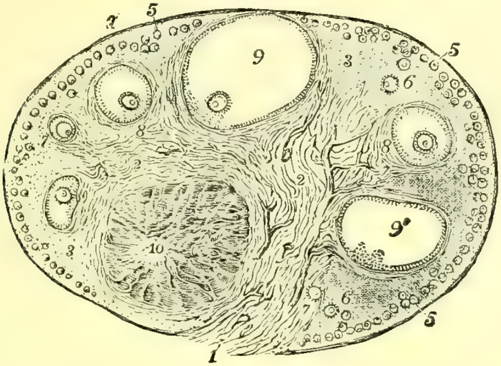


Fig. 393.—*View of a section of the prepared ovary of the cat.* 1, outer covering and free border of the ovary; 1', attached border; 2, the ovarian stroma, presenting a fibrous and vascular structure; 3, granular substance lying external to the fibrous stroma; 4, blood-vessels; 5, ovigerms in their earliest stages occupying a part of the granular layer near the surface; 6, ovigerms which have begun to enlarge and to pass more deeply into the ovary; 7, ovigerms round which the Graafian follicle and tunica granulosa are now formed, and which have passed somewhat deeper into the ovary and are surrounded by the fibrous stroma; 8, more advanced Graafian follicle with the ovum imbedded in the layer of cells constituting the proligerous disc; 9, the most advanced follicle containing the ovum, &c.; 9', a follicle from which the ovum has accidentally escaped; 10, corpus luteum. $\frac{6}{1}$. (Schrön.)

Structure.—The ovary is enveloped by a *capsule* of dense fibro-cellular tissue, covered on the outside by epithelium (germ-epithelium), the cells of which, although continuous with, and originally derived from, the squamous epithelium of the peritoneum, are short columnar.

The term *germ-epithelium* is used on account of the relation which it bears in early life to the development of the ova; the ova being formed by certain of these epithelial cells, which, becoming modified in structure, are gradually enclosed in the ovarian stroma. (Waldeyer.) (See fig. 394.)

The internal structure of the organ consists of a peculiar soft fibrous tissue, or *stroma*, abundantly supplied with blood-vessels, and having embedded in it, in various stages of development, numerous minute follicles or vesicles, the *Graafian vesicles*, or sacculi, containing the ova (fig. 394).

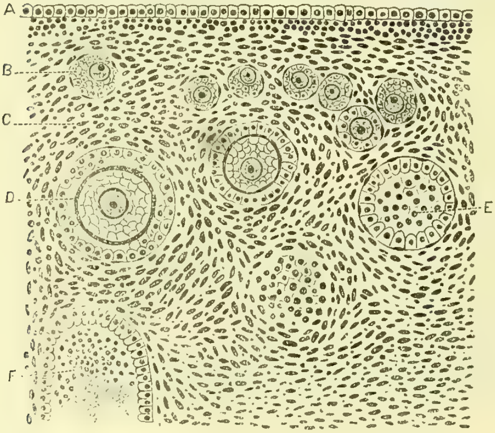


Fig. 391.—*Section of the ovary of a cat.* A, germinal epithelium; B, immature Graafian follicle; C, stroma of ovary; D, vitelline membrane containing the ovum; E, Graafian follicle showing lining cells; F, follicle from which the ovum has fallen out. (V. D. Harris.)

Graafian Vesicles. — If the human ovary be examined at any period between early infancy and advanced age, but especially during that period of life in which the power of conception exists, it will be found to contain a number of small vesicles or membranous sacs of various sizes; these have been already alluded to as the *follicles* or *vesicles* of *De Graaf*, the anatomist who first accurately described them; they are sometimes called *ovisacs*.

At their first formation, the Graafian vesicles are near the surface of the stroma of the ovary, but subsequently become more deeply placed; and, again, as they increase in size, make their way towards the surface (fig. 394).

When mature, they form little prominences on the exterior of the ovary, covered only by a thin layer of condensed fibrous tissue and epithelium. Each follicle has an external membranous envelope, comprised of fine fibrous tissue, and connected with the surrounding stroma of the ovary by networks of blood-vessels. This envelope or tunic is lined with a layer of nucleated cells, forming a kind of epithelium or internal tunic, and named *membrana granulosa.* The cavity of the follicle is filled with an albuminous fluid in which microscopic granules float; and it contains also the *ovum.*

Ovum.—The ovum is a minute spherical body situated, in immature follicles, near the centre; but in those nearer maturity, in contact with the membrana granulosa at that part of the follicle which forms a prominence on the surface of the ovary. The cells of the membrana-granuloso are at that point more numerous than elsewhere, and are heaped around the ovum, forming a kind of granular zone, the *discus proligerus* (fig. 395).

In order to examine an ovum, one of the Graafian vesicles, it matters not whether it be of small size or arrived at maturity, should be pricked, and the contained fluid received upon a slide. The ovum then, being found in the midst of the fluid by means of a simple lens, may be further examined with higher microscopic powers. Owing to its globular form, however, its structure cannot be seen until it is subjected to gentle pressure.

The human ovum measures about $\frac{1}{120}$ of an inch. Its external investment is a transparent membrane, about $\frac{1}{2500}$ of an inch in thickness, which under the microscope appears as a bright ring (4, fig. 395), bounded externally and internally by a dark outline; it is called the *zona pellucida,* or *vitelline membrane.* It adheres externally to the heap of cells constituting the *discus proligerus.* Within this transparent investment or zona pellucida, and usually in close contact with it, lies the yolk or vitellus, which is composed of granules and globules of various sizes, imbedded in a more or less fluid substance. The smaller granules, which are the more numerous, resemble in their appearance, as well as their constant motion, pigment-granules. The larger granules or globules, which have the aspect of fat-globules, are in greatest number at the periphery of the yolk. The number of the granules is, according

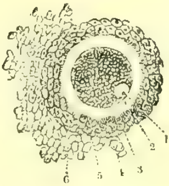


Fig. 395.—*Ovum of the sow.* 1, germinal spot; 2, germinal vesicle; 3, yolk; 4, zona pellucida; 5, discus proligerus; 6, adherent granules or cells. (Barry.)

to Bischoff, greatest in the ova of carnivorous animals. In the human ovum their quantity is comparatively small.

In the substance of the yolk is imbedded the *germinal vesicle*, or vesicula germinativa (2, fig. 395). This vesicle is of greatest relative size in the smallest ova, and is in them surrounded closely by the yolk, nearly in the centre of which it lies. During the development of the ovum, the germinal vesicle increases in size much less rapidly than the yolk, and comes to be placed near to its surface. It is about $\frac{1}{720}$ of an inch in diameter. It consists of a fine, transparent, structureless membrane, containing a clear, watery fluid, in which are sometimes a few granules; and at that part of the periphery of the germinal vesicle which is nearest to the periphery of the yolk is situated the *germinal spot* (*macula germinativa*), a finely granulated substance, of a yellowish colour, strongly refracting the rays of light, and measuring about $\frac{1}{3000}$ of an inch in diameter.

Such are the parts of which the Graafian follicle and its contents, including the ovum, are composed. With regard to the mode and order of development of these parts there is considerable uncertainty; but it seems most likely that the ovum is formed before the Graafian vesicle or ovisac.

With regard to the parts of the *ovum* first formed, it appears certain that the formation of the germinal vesicle precedes that of the yolk and zona pellucida, or vitelline membrane. Whether the germinal spot is formed first, and the germinal vesicle afterwards developed around it, cannot be decided in the case of vertebrate animals; but the observations of Kölliker and Bagge on the development of the ova of intestinal worms show that in these animals, the first step in the process is the production of round bodies resembling the germinal spots of ova, the germinal vesicles being subsequently developed around these in the form of transparent membranous cells.

From the earliest infancy, and through the whole fruitful period of life, there appears to be a constant formation, development, and maturation of Graafian vesicles, with their contained ova. Until the period of puberty, however, the process is comparatively inactive; for, previous to this period, the ovaries are small and pale, the Graafian vesicles in them are very minute, and probably never attain full development, but soon shrivel and disappear, instead of bursting, as matured follicles do; the contained ova are also incapable of being impregnated. But, coincident with the other changes which occur in the body at the time of puberty, the ovaries enlarge, and become very vascular, the formation of Graafian vesicles is more abundant, the size and degree of development attained by them are greater, and the ova are capable of being fecundated.

Fallopian Tubes.—The *Fallopian tubes* are about four inches in length, and extend between the ovaries and the upper angles of the uterus. At the point of attachment to the uterus, the Fallopian tube is very narrow; but in its course to the ovary it increases to about a line and a half in thickness; at its distal extremity, which is free and floating, it bears a number of *fimbriæ*, one of which, longer than the rest, is attached to the ovary. The canal by which each Fallopian tube is traversed is narrow, especially at its point of entrance into the uterus, at which it will scarcely admit a bristle; its other extremity is wider, and opens into the cavity of the abdomen, surrounded by the zone of fimbriæ. Externally, the Fallopian tube is invested with peritoneum; internally, its canal is lined with mucous membrane, covered with ciliated epithelium: between the peritoneal and mucous coats, the walls are composed, like those of the uterus, of fibrous tissue and plain muscular fibres.

Uterus.—The *Uterus* (*u*, *c*, fig. 392) is somewhat pyriform, and in the unimpregnated state is about three inches in length, two in breadth at its upper part or *fundus*, but at its lower pointed part or *neck*, only about half an inch. The part between the fundus and neck is termed the *body* of the uterus: it is about an inch in thickness.

Structure.—The uterus is constructed of three principal layers, or coats,—*serous*, *fibrous* and *muscular*, and *mucous*. (1.) The serous coat, which has the same general structure as the peritoneum, covers the organ before and behind, but is absent from the front surface of the neck. (2.) The middle coat is composed of dense connective tissue, with which are intermingled fibres of unstriped muscle. The latter become enormously developed during pregnancy. (3.) The mucous membrane of the uterus will be described more in detail presently (p. 745). It is lined by columnar ciliated epithelium, which extends also into the interior of the tubular glands, of which the mucous membrane is largely made up. (Allen Thomson, Nylander, Friedländer, John Williams.)

The cavity of the uterus corresponds in form to that of the organ itself: it is very small in the unimpregnated state; the sides of its mucous surface being almost in contact, and probably only separated from each other by mucus. Into its upper part, at each side, opens the canal of the corresponding Fallopian tube: below, it communicates with the vagina by a fissure-like opening in its neck, the *os uteri*, the margins of which are distinguished into two lips, an anterior and posterior. In the mucous membrane of the cervix are found several mucous follicles, termed ovula or glandulæ Nabothi: they probably form the jelly-like substance by which the os uteri is usually found closed.

The *vagina* is a membranous canal, five or six inches long, extending obliquely downwards and forwards from the neck of the uterus, which it embraces, to the external organs of generation. It is lined with mucous membrane, which in the ordinary contracted state of the canal is thrown into transverse folds. External to the mucous membrane the walls of the vagina are constructed of fibrous tissue, within which, especially around the lower part of the tube, is a layer of erectile tissue. The lower extremity of the vagina is embraced by an orbicular muscle, the *constrictor vaginæ;* its external orifice, in the virgin, is partially closed by a fold or ring of mucous membrane, termed the *hymen.* The external organs of generation consist of the *clitoris*, a small elongated body, situated above and in the middle line, and constructed, like the male penis, of two erectile corpora cavernosa, but unlike it, without a corpus spongiosum, and not perforated by the urethra; of two folds of mucous membrane, termed *labia interna*, or *nymphæ;* and, in front of these, of two other folds, the *labia externa*, or *pudenda*, formed of the external integument, and lined internally by mucous membrane. Between the nymphæ and beneath the clitoris is an angular space, termed the vestibule, at the centre of whose base is the orifice of the *meatus urinarius.* Numerous mucous follicles are scattered beneath the mucous membrane composing these parts of the external organs of generation; and at the side of the lower part of the vagina, are two larger lobulated glands, named *vulvo-vaginal*, or Duverney's glands, which are analogous to Cowper's glands in the male.

Discharge of the Ovum.—In the process of development of individual Graafian vesicles, it has been already observed, that as each increases in size, it gradually approaches the surface of the ovary, and when fully ripe or mature, forms a little projection on the exterior. Coincident with the increase of size, caused by the augmentation of its liquid contents, the external envelope of the distended vesicle becomes very thin and eventually bursts. By this means, the ovum and fluid contents of the Graafian vesicle are liberated, and escape on the exterior of the ovary, whence they pass into the Fallopian tube, the fimbriated processes of the extremity of which are supposed coincidentally to grasp the ovary, while the aperture of the tube is applied to the part corresponding to the matured and bursting vesicle.

In animals whose capability of being impregnated occurs at regular periods, as in the human subject, and most Mammalia, the Graafian vesicles and their contained ova appear to arrive at maturity, and the latter to be discharged at such periods only. But in other animals, *e.g.*, the common fowl, the formation, maturation, and discharge of ova appear to take place almost constantly.

It has long been known, that in the so-called oviparous animals, the separation of ova from the ovary may take place independently of impregnation by the male, or even of sexual union. And it is now established that a like maturation and discharge of ova, independently of coition, occurs in Mammalia, the periods at which the matured ova are separated from the ovaries and received into the Fallopian tubes being indicated in the lower Mammalia by the phenomena of *heat* or *rut:* in the human female, although not always with exact coincidence, by the phenomena of *menstruation.* If the union of the sexes take place, the ovum may be fecundated, and if no union occur it perishes.

That this maturation and discharge occur periodically, and only during the phenomena of heat in the lower Mammalia, is made probable by the facts that, in all instances in which Graafian vesicles have been found presenting the appearance of recent rupture, the animals were at the time, or had recently been. in heat ; that on the other hand, there is no authentic and detailed account of Graafian vesicles being found ruptured in the intervals of the period of heat; and that female animals do not admit the males, and never become impregnated, except at those periods.

Menstruation.—Many circumstances make it certain that the human female is subject, in these respects, to the same law as the females of other mammiferous animals; namely, that in her as in them, ova are matured and discharged from the ovary independent of sexual union. This maturation and discharge occur, moreover, periodically at or about the epochs of menstruation. Thus Graafian vesicles recently ruptured have been frequently seen in ovaries of virgins or women who could not have been recently impregnated; and although it is true that the ova discharged under these circumstances have rarely been discovered in the Fallopian tube, partly on account of their minute size, and partly because the search has seldom been prosecuted with much care, yet analogy forbids us to doubt that in the human female, as in the domestic quadrupeds, the result and purpose of the rupture of the follicles is the discharge of the ova.

The evidence of the periodical discharge of ova is that in most cases in which signs of menstruation have been found in the uterus, follicles in a state of maturity or of rupture have been seen in the ovary; and that although conception is not confined to the periods of menstruation, yet it is more likely to occur about a menstrual epoch than at other times.

The exact relation between the discharge of ova and menstruation is not very clear. It was generally believed that the monthly flux was the result of a congestion of the uterus arising from the enlargement and rupture of a Graafian follicle; but though a Graafian follicle is, as a rule, ruptured at each menstrual epoch, yet several instances are recorded in which menstruation has occurred where no Graafian follicle has been ruptured, and on the other hand cases are known where ova have been discharged in amenorrhœic women. It must therefore be admitted that menstruation is not dependent on the maturation and discharge of ova.

It was, moreover, generally understood that ova were discharged towards the close or soon after the cessation of a menstrual flow. Observations made after death, and facts obtained by clinical investigation, however, do not support this view. (Reichert, J. Williams, Löwenthal.) Rupture of a Graafian follicle does not happen on the same day of the monthly period in all women. It may occur towards the close or soon after the cessation of a flow; but only in a small minority of the subjects examined after death was this the case. On the other hand, in almost all such subjects of which there is record, rupture of the follicle appears to have taken place before the commencement of the catamenial flow. Moreover, the custom of the Jews—a prolific race, to whom by the Levitical law sexual intercourse during the week following menstruation was forbidden—militates strongly in favour of the view that conception usually occurs before and not soon after a menstrual epoch, and necessarily, therefore, for the view that ova are usually discharged before the catamenial flow. This, together with the anatomical condition of the uterus just before the catamenia, seem to indicate that the ovum fertilized is that which is discharged in connection with the first absent, and not that with the last present menstruation. (Kundrat.)

Though menstruation does not appear to depend upon the discharge of ova, yet the presence of the ovaries seems necessary for the performance of the function; for women do not menstruate when both ovaries have been removed by operation. Some instances have been recently recorded, indeed, of a sanguineous discharge, occurring periodically from the vagina after both ovaries have been previously removed for disease; and it has been inferred from this that menstruation is a function independent of the ovary: but this evidence is not conclusive, inasmuch as it is possible that portions of ovarian tissue were left after the operation.

Characters of Menstrual Discharge.—The menstrual discharge is a thin sanguineous fluid, having a peculiar odour. It is of a dark colour, and consists of blood, epithelium, and mucus from the uterus and vagina, serum, and the débris of a membrane called the *decidua menstrualis.* This membrane is the developed mucous surface of the body of the uterus. It does not extend into the Fallopian tube or into the cavity of the cervix. It attains its highest state of development in the unimpregnated organ just before the commencement of a catamenial flow (fig. 396). If impregnation take place, it becomes the *decidua vera;* if impregnation fail, the membrane undergoes rapid disintegration; its vessels are laid open and hæmorrhage follows (John Williams).

The blood poured out does not coagulate in consequence partly of the admixture already mentioned, or, very possibly, coagulation occurs, but the process is more or less spoiled, and what clot is formed is broken down again, so as to imitate liquid blood. (See also p. 91.)

Fig. 396.

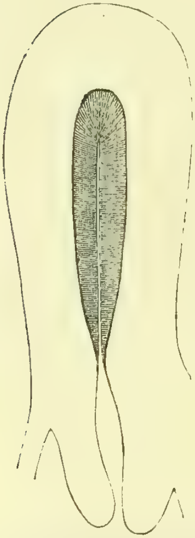


Fig. 397.

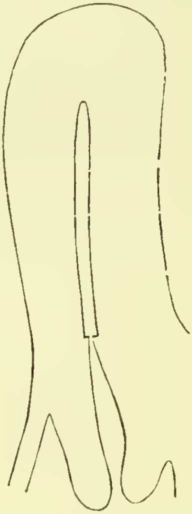


Fig. 398.

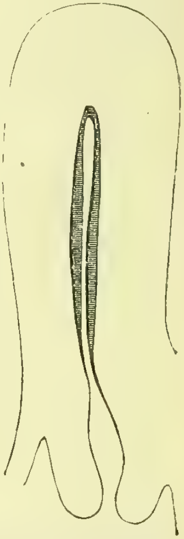


Fig. 396.—*Diagram of uterus just before menstruation*; the shaded portion represents the thickened mucous membrane. Fig. 397.—*Diagram of uterus when menstruation has just ceased*, showing the cavity of the uterus deprived of mucous membrane. Fig. 398.—*Diagram of uterus a week after the menstrual flux has ceased:* the shaded portion represents renewed mucous membrane. (J. Williams.)

Menstruation, therefore, is not the result of congestion, or of a species of erection, but of a destructive process by which the *decidua* or *nidus* prepared for an impregnated ovum is carried away. It is not a sign of the capability of being impregnated as much as of disappointed impregnation.

The occurrence of a menstrual discharge is one of the most prominent indications of the commencement of puberty in the female sex; though its absence even for several years is not necessarily attended with arrest of the other characters of this period of life, or with inaptness for sexual union, or incapability of impregnation. The average time of its first appearance in females of this country and others of about the same latitude, is from fourteen to fifteen; but it is much influenced by the kind of life to which girls are subjected, being accelerated by habits of luxury and indolence, and retarded by contrary conditions. On the whole, its appearance is earlier in persons dwelling in warm climes than in those inhabiting colder latitudes; though the extensive investigations of Robertson show that the influence of temperature on the development of puberty has been exaggerated. Much of the influence attributed to climate appears due to the custom prevalent in many hot countries, as in Hindostan, of giving girls in marriage at a very early age, and inducing sexual excitement previous to the proper menstrual time. The menstrual functions continue through the whole fruitful period of a woman's life, and usually cease between the forty-fifth and fiftieth years.

The several menstrual periods usually occur at intervals of a lunar month, the duration of each being from three to six days. In some women the intervals are as short as three weeks or even less; while in others they are longer than a month. The periodical return is usually attended by pain in the loins, a sense of fatigue in the lower limbs, and other symptoms, which are different in different individuals. Menstruation does not usually occur in pregnant women, or in those who are suckling; but instances of its occurrence in both these conditions are by no means rare.

Corpus Luteum.

Immediately before, as well as subsequent to, the rupture of a Graafian vesicle, and the escape of its ovum, certain changes ensue in the interior of the vesicle, which result in the production of a yellowish mass, termed a *Corpus luteum.*

When fully formed the corpus luteum of mammiferous animals is a roundish solid body, of a yellowish or orange colour, and composed of a number of lobules, which surround, sometimes a small cavity, but more frequently a small stelliform mass of white substance, from which delicate processes pass as septa between the several lobules. Very often, in the cow and sheep, there is no white substance in the centre of the corpus luteum; and the lobules projecting from the opposite walls of the Graafian vesicle appear in a section to be separated by the thinnest possible lamina of semi-transparent tissue.

When a Graafian vesicle is about to burst and expel the ovum, it becomes highly vascular and opaque; and, immediately before the rupture takes place, its walls appear thickened on the interior by a reddish glutinous or fleshy-looking substance. Immediately after the rupture, the inner layer of the wall of the vesicle appears pulpy and flocculent. It is thrown into wrinkles by the contraction of the outer layer, and, soon, red fleshy mammillary processes grow from it, and gradually enlarge till they nearly fill the vesicle, and even protrude from the orifice in the external covering of the ovary. Subsequently this orifice closes, but the fleshy growth within still increases during the earlier period of pregnancy, the colour of the substance gradually changing from red to yellow, and its consistence becoming firmer.

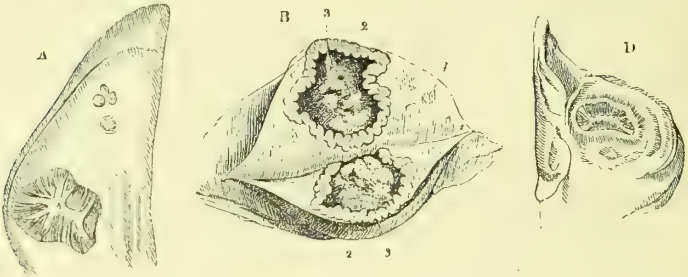


Fig. 399.—*Corpora lutea of different periods.* B. Corpus luteum of about the sixth week after impregnation, showing its plicated form at that period. 1, substance of the ovary; 2, substance of the corpus luteum; 3, a greyish coagulum in its cavity. (Paterson.) A, corpus luteum two days after delivery; D, in the twelfth week after delivery. (Montgomery.)

The corpus luteum of the human female (fig. 399) differs from that of the domestic quadruped in being of a firmer texture, and having more frequently a persistent cavity at its centre, and in the stelliform cicatrix, which remains in the cases where the cavity is obliterated, being proportionately of much larger bulk. The quantity of yellow substance formed is also much less: and, although the deposit increases after the vesicle has burst, yet it does not usually form mammillary growths projecting into the cavity of the vesicle, and never protrudes from the orifice, as is the case in other Mammalia. It maintains the character of a uniform, or nearly uniform, layer, which is thrown into wrinkles, in consequence of the contraction of the external tunic of the vesicle. After the orifice of the vesicle has closed, the growth of the yellow substance continues during the first half of pregnancy, till the cavity is reduced to a comparatively small size, or is obliterated;

in the latter case, merely a white stelliform cicatrix remains in the centre of the corpus luteum.

An effusion of blood generally takes place into the cavity of the Graafian vesicle at the time of its rupture, especially in the human subject, but it has no share in forming the yellow body ; it gradually loses its colouring matter, and acquires the character of a mass of fibrin. The serum of the blood sometimes remains included within a cavity in the centre of the coagulum, and then the decolorised fibrin forms a membraniform sac, lining the corpus luteum. At other times the serum is removed, and the fibrin constitutes a solid stelliform mass.

The yellow substance of which the corpus luteum consists, both in the human subject and in the domestic animals, is a growth from the inner surface of the Graafian vesicle, the result of an increased development of the cells forming the membrana granulosa, which naturally lines the internal tunic of the vesicle.

The first changes of the internal coat of the Graafian vesicle in the process of formation of a corpus luteum, seem to occur in every case in which an ovum escapes; as well in the human subject as in the domestic quadrupeds. If the ovum is impregnated, the growth of the yellow substance continues during nearly the whole period of gestation and forms the large corpus luteum commonly described as a characteristic mark of impregnation. If the ovum is not impregnated, the growth of yellow substance on the internal surface of the vesicle proceeds, in the human ovary, no further than the formation of a thin layer, which shortly disappears; but in the domestic animals it continues for some time after the ovum has perished, and forms a corpus luteum of considerable size. The fact that a structure, in its essential characters similar to, though smaller than, a corpus luteum observed during pregnancy, is formed in the human subject, independent of impregnation or of sexual union, coupled with the varieties in size of corpora lutea formed during pregnancy, necessarily renders unsafe all evidence of previous impregnation founded on the existence of a corpus luteum in the ovary.

The following table by Dalton, expresses well the differences between the corpus luteum of the pregnant and unimpregnated condition respectively.

	Corpus Luteum of Menstruation.	Corpus Luteum of Pregnancy.
At the end of three weeks	Three-quarters of an inch in diameter; central clot reddish; convoluted wall pale.	
One month .	Smaller; convoluted wall bright yellow; clot still reddish.	Larger; convoluted wall bright yellow; clot still reddish.
Two months.	Reduced to the condition of an insignificant cicatrix.	Seven-eighths of an inch in diameter; convoluted wall bright yellow; clot perfectly decolorised.
Six months .	Absent.	Still as large as at end of second month; clot fibrinous; convoluted wall paler.
Nine months.	Absent.	One-half an inch in diameter; central clot converted into a radiating cicatrix; the external wall tolerably thick and convoluted, but without any bright yellow colour.

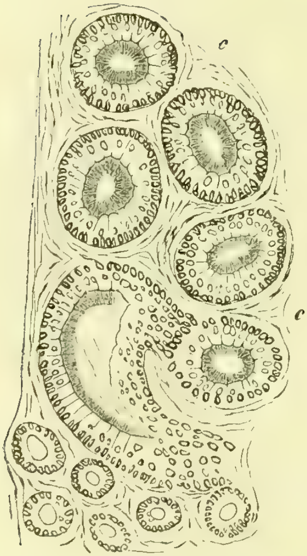


Fig. 400.—*Section of dog's epididymis.* The tube is cut in several places, both transversely and obliquely; it is seen to be lined by a ciliated epithelium, the nuclei of which are well shown. *c*, connective tissue. (Schofield.)

IMPREGNATION OF THE OVUM.

Male Sexual Functions.

Testes.—The fluid of the male, by which the ovum is impregnated, consists essentially of the semen secreted by the *testicles:* and to this are added, as necessary, perhaps to its perfection, a material secreted by the *vesiculæ seminales,* as well as the secretion of the prostate gland, and of Cowper's glands. Portions of these several fluids are, probably all discharged, together with the proper secretion of the testicles.

The secreting structure of the testicle and its duct are disposed of in two contiguous parts, (1) the body of the testicle enclosed within a tough fibrous membrane, the *tunica albuginea,* on the outer surface of which is the serous covering formed by the *tunica vaginalis*, and (2) the *epididymis* and *vas deferens.*

Vas Deferens.—The *vas deferens*, or duct of the testicle, which is about two feet in length, is constructed externally of connective tissue, and internally is lined by mucous membrane, covered by columnar epithelium ; while between these two coats is a middle coat, very firm and tough, made up chiefly of longitudinal with some circular plain muscular fibres. When followed back to its origin, the vas deferens is found to pass to the lower part of the *epididymis*, with which it is directly continuous (fig. 402), and assumes there a much smaller diameter with an exceedingly tortuous course.

The *epididymis*, which is lined, except at its lowest part, by columnar ciliated epithelium (fig. 400), is commonly described as consisting (fig. 402) of a *globus minor* (*g*), the *body* (*e*), and the *globus major* (*l*). When unravelled, it is found to be constructed of a single tube, measuring about twenty feet in length.

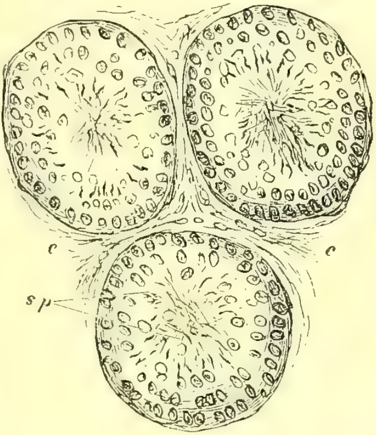


Fig. 401.—*A section of dog's testicle*, highly magnified, showing three "tubuli seminiferi," lined and largely occupied by a spheroidal epithelium, the numerous nuclei of which are well seen ; *c*, connective tissue surrounding and supporting the tubuli ; *sp*, masses of spermatozoa occupying the centre of tubuli : the small black bodies scattered about are the heads of the spermatozoa. (Schofield.)

At the globus major this duct divides into ten or twelve small branches, the convolutions of which form coniform masses, named *coni vasculosi ;* and the ducts continued from these, the *vasa efferentia*, after anastomosing, one with another in what is called the *rete testis*, lead finally as the *tubuli recti* or *vasa recta* to the *tubules* which form the proper substance of the testicle, wherein they are arranged in lobules, closely packed, and all attached to the tough fibrous tissue at the back of the testicle. The epithelium of the coni vasculosi and vasa efferentia is columnar and ciliated ; that of the rete testis is squamous.

Structure of Seminal Tubes.—The seminal tubes, or *tubuli seminiferi*, which compose the parenchyma of the testicle, are arranged in lobules between the connective tissue septa.

They are relatively large, very wavy, and much convoluted; and they possess a few lateral branches, by which they become connected into a network. They form terminal loops, and in the peripheral portion of the testis the tubules are possessed of minute lateral cæcal branchlets.

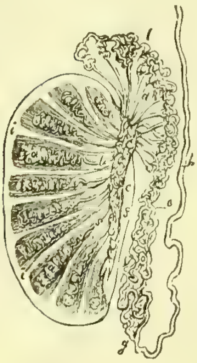


Fig.402.—*Plan of a vertical section of the testicle*, showing the arrangement of the ducts. The true length and diameter of the ducts have been disregarded. *a, a*, tubuli seminiferi coiled up in the separate lobes; *b*, tubuli recti or vasa recta; *c*, rete testis; *d*, vasa efferentia ending in the coni vasculosi; *l, e, g*, convoluted canal of the epididymis; *h*, vas deferens; *f*, section of the back part of the tunica albuginea; *i. i*, fibrous processes running between the lobes; *s*, mediastinum.

Each seminal tubule in the adult testis is limited by a membrana propria, which appears as a hyaline elastic membrane containing oval flattened nuclei at regular intervals. Inside this membrana propria are several layers of epithelial cells, the *seminal cells*. These consist of an inner and outer layer, the latter being situated next the membrana propria. These cells are of two kinds, those that are in a resting state and those that are in a state of division. The latter are called mother cells, and the smaller cells resulting from their division are called daughter cells or spermatoblasts. From these the spermatozoa are formed. During their development they lie in groups, but when fully formed they become detached and fill the lumen of the seminiferous tubule (fig. 401).

Spermatozoa.—On examining the spermatozoon of Triton cristatus, one of the Amphibia which possess the largest of all Vertebrate animals, Heneage Gibbes found that the organism (fig. 404) consisted of (*a*) a long pointed head, at the base of which is (*b*), an elliptical structure joining the head to (*c*), a long filiform body; (*d*), a fine filament, much longer than the body, is connected with this latter by (*e*), a homogeneous membrane.

The head, as it appears in the fresh specimen, has a different refractive power from that of the rest of the organism, and with a high power appears to be a light green colour; there is also a central line running up it, from which it appears to be hollow. The elliptical structure at the base of the head connects it with the long thread-like body, and the filament springs from it. Whilst the spermatozoon is living, this filament is in constant motion; at first this is so quick that it is difficult to see it, but as its vitality becomes impaired the motion gets slower, and it is then easily perceived to be a continuous waving from side to side.

In Man the head (fig. 405) is club-shaped, and from its base springs the very delicate filament which is three or four times as long as the body; and the membrane which attaches it to the body is much broader, and allows it to lie at a greater distance from the body than in the spermatozoa of any other Mammal examined.

Gibbes concludes :—1st. That the head of the spermatozoon is enclosed in a sheath, which is a continuation of the membrane which surrounds the filament and connects it to the body, acting in fact the part of a mesentery. 2ndly. That the substance of the head is quite distinct in its composition from the elliptical structure, the filament and the long body, and that it is readily acted upon by alkalies; these re-agents have no effect, however, on the other part, excepting the membranous sheath. 3rdly. That this elliptical structure has its analogue in the Mammalian spermatozoon; in the one case the head is drawn out as a long pointed process, in the other it is of a globular form, and surrounds the elliptical structure. 4thly. That the motive power lies, in a great measure, in the filament and the membrane attaching it to the body.

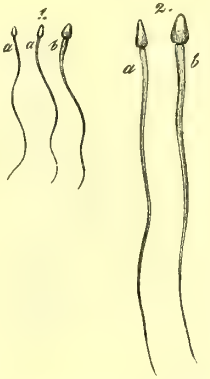


Fig. 403. — *Spermatic filaments from the human vas deferens.* 1, magnified 350 diameters; 2, magnified 800 diameters; *a*, from the side; *b*, from above. (From Kölliker.)

The occurrence of spermatozoa in the impregnating fluid of nearly all classes of animals proves that they are essential to the process of impregation, and their actual contact with the ovum is necessary for its development; but concerning the manner of their action nothing is known.

The seminal fluid is, probably, after the period of puberty, secreted constantly, though, except under excitement, very slowly, in the tubules of the testicles. From these, it passes along the vasa deferentia into the vesiculæ seminales, whence, if not expelled in emission, it may be discharged, as slowly as it enters them, either with the urine, which may remove minute quantities, mingled with the mucus of the bladder and the secretion of the prostate, or from the urethra in the act of defæcation.

Vesiculæ Seminales—The *vesiculæ seminales* (fig. 406) have the appearance of outgrowths from the vasa deferentia. Each vas deferens, just before it enters the prostate gland, through part of which it passes to terminate in the urethra, gives off a side-branch, which bends back from it at an acute angle: and this branch dilating, variously branching, and pursuing in both itself and its branches a tortuous course, forms the vesicula seminalis.

Structure.—Each of the vesiculæ, therefore, might be unravelled into a single branching tube, sacculated, convoluted, and folded up. The structure of the vesiculæ resembles closely that of the vasa deferentia. The mucous membrane lining the vesiculæ seminales, like that of the gall-bladder, is minutely wrinkled and set with folds and ridges arranged so as to give it a finely reticulated appearance.

Functions. — To the vesiculæ seminales a double function may be assigned; for they both secrete some fluid to be added to that of the testicles, and serve as reservoirs for the seminal fluid. The former is their most constant and probably most important office;

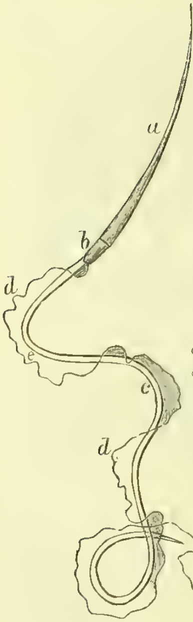


Fig. 404.

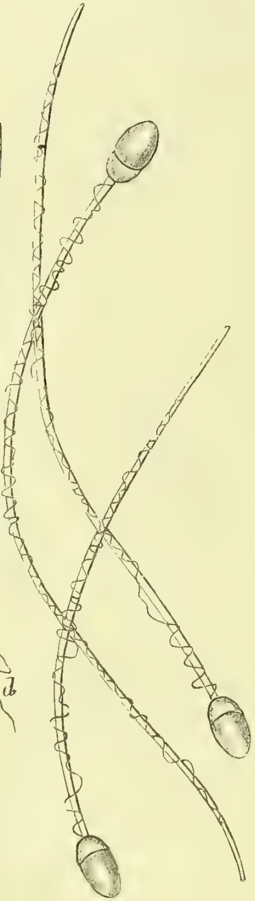


Fig. 405.

Fig. 404.—*Spermatozoon of Salamandra Maculata.* Fresh mounted in glycerin. × 950, reduced one half.
Fig. 405.—*Human spermatozoa.* × 2500. (H. Gibbes.)

for in the horse, bear, guinea-pig, and several other animals, in whom the vesiculæ seminales are large and of apparently active function, they do not communicate with the vasa deferentia, but pour their secretions, separately, though it may be simultaneously, into the urethra. In man, also, when one testicle is lost, the corresponding vesicula seminalis suffers no atrophy, though its function as a reservoir is abrogated. But how the vesiculæ seminales act as secreting organs is unknown; the peculiar brownish fluid which they contain after death does not properly represent their secretion, for it is different in appearance from anything discharged during life, and is mixed with semen. It is nearly certain, however, that their secretion contributes to the proper composition of the impregnating fluid; for in all the animals in whom they exist, and in whom the generative functions are exercised at only one season of the year, the vesiculæ seminales, whether they communicate with the vasa deferentia or

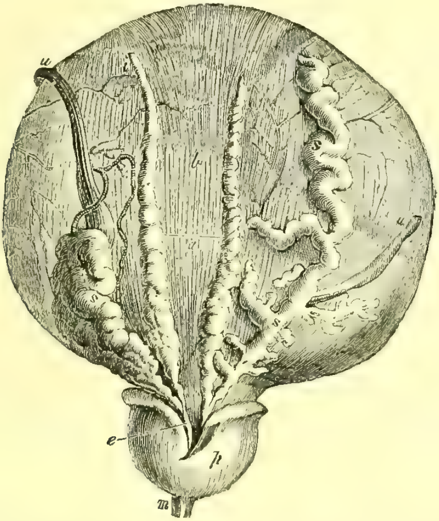


Fig. 406.—*Dissection of the base of the bladder and prostate gland, showing the vesiculæ seminales and vasa deferentia.* *a*, lower surface of the bladder at the place of reflexion of the peritoneum; *b*, the part above covered by the peritoneum; *i*, left vas deferens, ending in *e*, the ejaculatory duct; the vas deferens has been divided near *i*, and all except the vesicle portion has been taken away; *s*, left vesicula seminalis joining the same duct; *s*, *s*, the right vas deferens and right vesicula seminalis, which has been unravelled; *p*, under side of the prostate gland; *m*, part of the urethra; *u*, *u*, the ureters (cut short), the right one turned aside. (Haller.)

not, enlarge commensurately with the testicles at the approach of that season.

That the vesiculæ are also reservoirs in which the seminal fluid may lie for a time previous to its discharge, is shown by their commonly containing the seminal filaments in larger abundance than any portion of the seminal ducts themselves do. The fluid-like mucus, also, which is often discharged from the vesiculæ in straining during defæcation, commonly contains seminal filaments. But no reason can be given why this office of the vesiculæ should not be equally necessary to all the animals whose testicles are organised like those of man, or why in many animals the vesiculæ are wholly absent.

There is an equally complete want of information respecting the secretions of the prostate and Cowper's glands, their nature and purposes. That they contribute to the right composition of the impregnating fluid, is shown both by the position of the glands and by their enlarging with the testicles at the approach of an animal's breeding time. But that they contribute only a subordinate part is shown by the fact, that, when the testicles are lost, though these other organs be perfect, all procreative power ceases.

The Semen.

The mingled secretions of all the organs just described, form the *semen*, which is a thick whitish fluid composed of a *liquor seminis* and *spermatozoa*, with detached epithelial cells. The fluid part has not been satisfactorily analysed: but Henle says it contains fibrin, because shortly after being discharged, flocculi form in it by spontaneous coagulation, and leave the rest of it thinner and more liquid, so that the filaments move in it more actively.

Nothing has shown what it is that makes this fluid with its corpuscles capable of impregnating the ovum, or (what is yet more remarkable) of giving to the developing offspring all the characters, in features, size, mental disposition, and liability to disease, which belong to the father. This is a fact wholly inexplicable: and is, perhaps, only exceeded in strangeness by those facts which show that the seminal fluid may exert such an influence, not only on the ovum which it impregnates, but, through the medium of the mother, on many which are subsequently impregnated by the seminal fluid of another male.

It has been often observed that a well-bred bitch, if she have been once impregnated by a mongrel dog, will not bear thorough-bred puppies in the next two or three litters after that succeeding the copulation with the mongrel. But the best instance of the kind was in the case of a mare belonging to Lord Morten, who, while he was in India, wished to obtain a cross-breed between the horse and the quagga, and caused this mare to be covered by a male quagga. The foal that she next bore had the distinct marks of the quagga, in the shape of its head, black bars on the legs and shoulders, and other characters. After this time she was thrice covered by horses, and every time the foal she bore had still distinct, though decreasing, marks of the quagga; the peculiar characters of the quagga being thus impressed not only on the ovum then impregnated, but on the three following ova impregnated by horses. It would appear, therefore, that the constitution of an impregnated female may become so altered and tainted with the peculiarities of the impregnating male, through the medium of the fœtus, that she necessarily imparts such peculiarities to any offspring she may subsequently bear by other males. Of the direct means by which a peculiarity of structure on the part of a male is thus transmitted, nothing whatever is known.

As bearing upon this subject, the following note kindly given to the Editors by Mr. S. Probart may be added :—On the Farm Wellwood, the property of Charles R——, Esq., in the Division of Graaff Remet, Cape of Good Hope, there is at present running an aged mare with a numerous progeny. Some years ago she foaled for three successive seasons to a donkey; after that she gave birth to a mare foal, to a horse. This filly was a chestnut, and did not exhibit any taint of the donkey by which her dam had previously foaled. But when *she* in her turn foaled to a horse, *her* young bore the distinct marks along the back and withers, and rings round the lower parts of the legs, which are the peculiarity of the ass and the mule. Three foals she has had are all so marked.

Development.

Changes in the Ovum up to formation of the Blastoderm.

The earlier stages in development are so fundamentally similar in all vertebrate animals, from Fishes up to Man, that the gaps existing in our knowledge of the process in the higher Mammalia, such as man, may be in part, at any rate, filled up by the more accurate knowledge which we possess of the development of the ovum in such animals as the trout, frog, and fowl.

One important distinction between the ova of various Vertebrata should be remembered. In the hen's egg, besides the shell and the white or albumen, two other structures are to be distinguished—the *germ*, often called the cicatricula or "tread," and the *yelk* enclosed in its vitelline membrane.

The *germ* is essentially a cell, consisting of protoplasm enclosing a nucleus and nucleolus. It alone participates in the process of *segmentation* (to be immediately described), the great mass of the yelk (food-yelk) remaining quite unaffected by it. Since only the germ, which forms but a small portion of the yelk, undergoes segmentation, the ovum is called *meroblastic*.

In the Mammalia, on the other hand, there is no large unsegmented mass corresponding to the food-yelk of birds; the entire ovum undergoes segmentation, and is hence termed *holoblastic*.

The eggs of Fishes, Reptiles, and Birds, are meroblastic, while those of Amphibia and Mammalia are holoblastic.

Of the changes which the mammalian ovum undergoes previous to the formation of the embryo, some occur while it is still in the ovary, and are apparently independent of impregnation: others take place after it has reached the Fallopian tube. The knowledge we possess of these changes is derived almost exclusively from observations on the ova of the bitch and rabbit: but it may be inferred that analogous changes ensue in the human ovum.

Bischoff describes the yelk of an ovarian ovum soon after coitus as being unchanged in its characters, with the single exception of being fuller and more dense; it is still granular, as before, and does not possess any of the cells subsequently found in it. The germinal vesicle always disappears, sometimes before the ovum leaves the ovary, at other times not until it has entered the Fallopian tube; but always before the commencement of the metamorphosis of the yelk.

As the ovum approaches the middle of the Fallopian tube, it begins to receive a new investment, consisting of a layer of transparent albuminous or glutinous substance, which forms upon the exterior of the zona pellucida. It is at first exceedingly fine, and, owing to this, and to its transparency, is not easily recognised: but at the lower part of the Fallopian tube it acquires considerable thickness.

Segmentation.—The first visible result of fertilisation is a slight amœboid movement in the protoplasm of the ovum: this has been observed in some fish, in the frog, and in some mammals. Immediately succeeding to this the process of *segmentation* commences, and is completed during the passage of the ovum through the Fallopian tube. The yelk becomes constricted in the middle, and surrounded by a furrow which gradually deepening, at length cuts the yelk in half, while the same process begins almost immediately in each half of the yelk, and cuts it also in two. The same process is repeated in each of the quarters, and so on, until at last by continual cleavings, the whole yelk is changed into a mulberry-like-mass of small and more or less rounded bodies, sometimes called "vitelline spheres," the whole still enclosed by the *zona pellucida* or *vitelline membrane* (fig. 406*). Each of these little spherules contains a transparent vesicle, like an oil-globule, which is seen with difficulty, on account of its being enveloped by the yelk-granules which adhere closely to its surface.

The cause of this singular subdivision of the yelk is quite obscure: though the immediate agent in its productions seems to be the central vesicle contained in each division of the yelk. Originally there was probably but one vesicle, situated in the centre of the entire granular mass of the yelk, and probably derived from the germinal vesicle. This divides and subdivides: each successive division and subdivision of the vesicle being accompanied by a corresponding division of the yelk.

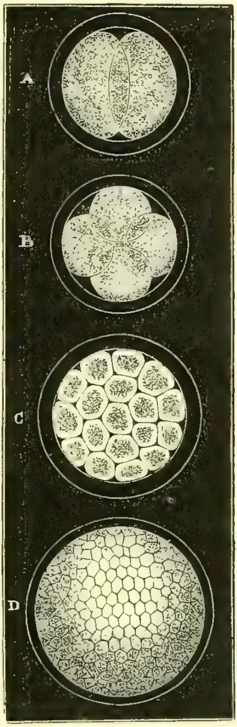


Fig. 406*. — *Diagrams of the various stages of cleavage of the yelk* (Dalton).

About the time at which the Mammalian ovum reaches the uterus, the process of division and subdivision of the yelk appears to have ceased, its substance having been resolved into its ultimate and smallest divisions, while its surface presents a uniform finely-granular-aspect, instead of its late mulberry-like appearance. The ovum, indeed, appears at first sight to have lost all trace of the cleaving process, and, with the exception of being paler and more translucent, almost exactly resembles the ovarian ovum, its yelk consisting apparently of a confused mass of finely granular substance. But on a more careful examination, it is found that these granules are aggregated into numerous minute spheroidal masses, each of which contains a clear vesicle or nucleus in its centre, and is, in fact, an "embryonal cell." The zona pellucida, and the layer of albuminous matter surrounding it, have at this time the same character as when at the lower part of the Fallopian tube.

The passage of the ovum, from the ovary to the uterus, occupies probably eight or ten days in the human female.

When the peripheral cells, which are formed first, are fully developed, they arrange themselves at the surface of the yelk into a kind of membrane, and at the same time assume a polyhedral shape from mutual pressure, so as to resemble pavement epithelium. The deeper cells of the interior pass gradually to the surface and accumulate there, thus increasing the thickness of the membrane already formed by the more superficial layer of cells, while the central part of the yelk remains filled only with a clear fluid. By this means the yelk is shortly converted into a kind of secondary vesicle, the walls of which are composed externally of the original vitelline membrane, and within by the newly formed cellular layer, the *blastodermic* or *germinal* membrane, as it is called.

Layers of the Blastoderm.—Before long the blastoderm is found to consist of three fundamental layers, *Epiblast, Mesoblast,* and *Hypoblast.*

The way in which these are formed may be readily studied in a hen's egg. In a freshly laid hen's egg, before incubation has commenced, the blastoderm is found to consist of two layers, fig. 407, *S* and *D*), the upper of which forms a distinct membrane of columnar cells, while the lower stratum consists of larger cells irregularly arranged.

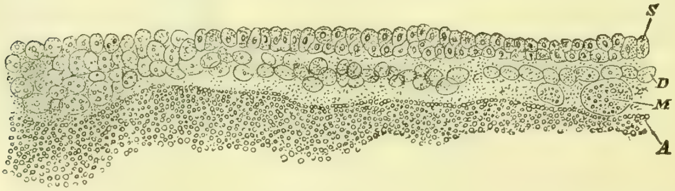


Fig. 407.—*Vertical section of area pellucida*, and *area opaca* (left extremity of figure) of blastoderm of a fresh-laid egg (unincubated). *S*, superficial layer corresponding to epiblast; *D*, deeper layer, corresponding to hypoblast, and probably in part to mesoblast; *M*, large "formative cells," filled with yelk granules, and lying on the floor of the segmentation cavity; *A*, the white yelk immediately underlying the segmentation cavity (Stricker).

Beneath the blastoderm there are a few scattered larger cells—"formative cells." In the lower of the above two layers, some cells become flattened and unite to form a distinct membrane (hypoblast); the remaining cells of the lower layer, together with some of the large formative cells, which migrate by amœboid movement round the edge of the hypoblast (fig. 408 *M*,), constitute a third layer (mesoblast).

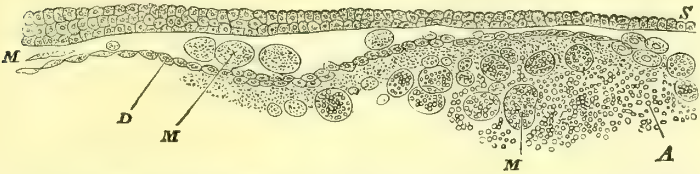


Fig. 408.—*Vertical section of blastoderm of chick* (1st day of incubation). *S*, epiblast, consisting of short columnar cells; *D*, hypoblast, consisting of a single layer of flattened cells; *M*, "formative cells." They are seen on the right of the figure, passing in between the epiblast and hypoblast to form the mesoblast; *A*, white yelk granules. Many of the large "formative cells" are seen containing these granules (Stricker).

These important changes are among the earliest results of incubation.

From the *epiblast* are ultimately developed the epidermis and its various appendages, also the cerebro-spinal *nerve centres*, the sensorial epithelium of the organs of special sense (eye, ear, nose), and the epithelium of the mouth and salivary glands.

From the *hypoblast* is developed the epithelium of the whole digestive canal together with that lining the ducts of all the glands which open into it; also the glandular parenchyma of the glands (*e.g.*, liver and pancreas) connected with it, and the epithelium of the respiratory track.

From the *mesoblast* are derived all the tissues and organs of the body intervening between these two, the whole group of the connective tissues, the muscles and the cerebro-spinal and sympathetic *nerves*, with the vascular and genito-urinary systems. and all the digestive canal with its various appendages with the exception of the lining epithelium above mentioned.

First rudiments of the Embryo and its chief organs.

Germinal area.—The position in which the embryo is about to appear is early marked out by a central roundish opacity in the blastoderm, due to the accumulation of cells in this region. This *germinal area*, which is at first circular, changes its shape becoming pyriform, and finally an elongated oval constricted in the middle like a savoy biscuit.

The central portion becomes transparent, and thus we have an *area pellucida*, surrounded by an *area opaca* (fig. 409).

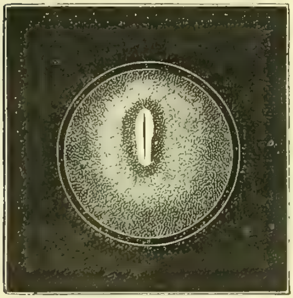


Fig. 409.—*Impregnated egg, with commencement of formation of embryo;* showing the area germinativa or embryonic spot, the area pellucida, and the primitive groove or trace (Dalton).

Primitive Groove.—The first trace of the embryo is a shallow longitudinal groove (*primitive groove*), which appears towards the posterior part of the area pellucida (figs. 409, 412).

Medullary Groove.—The primitive groove is but transitory, and is soon displaced by the *medullary groove*, which first appears at the anterior extremity of the future embryo, and grows backwards gradually causing the disappearance of the primitive groove.

Laminæ dorsales.— The medullary canal is bounded by two longitudinal elevations (*laminæ dorsales*) which are folds consisting entirely of cells of the epiblast: these grow up and arch over the medullary groove (fig. 411) till they coalesce in the middle line, converting it from an open furrow into a closed tube—the primitive cerebro-spinal axis. Over this closed tube, the walls of which consist of more or less cylindrical cells, the superficial layer of the epiblast is now continued as a distinct membrane.

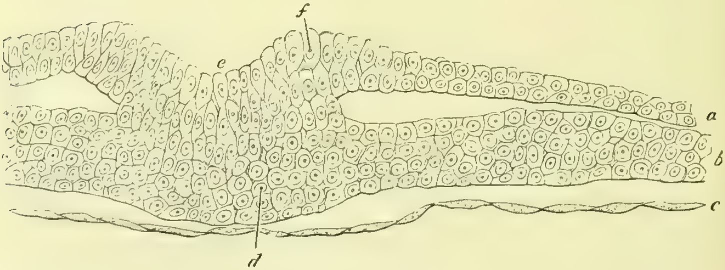


Fig. 410.—*Transverse section through embryo chick* (26 hrs.). *a*, epiblast; *b*, mesoblast; *c*, hypoblast; *d*, central portion of mesoblast, which is here fused with epiblast; *e*, primitive groove; *f*, dorsal ridge (Klein).

The union of the medullary folds or laminæ dorsales takes place first about the neck of the future embryo; they soon after unite over the region of the head, while the closing in of the groove progresses much more slowly towards the hinder extremity of the embryo. The medullary groove is by no means of uniform diameter throughout, but even before the dorsal laminæ have united over it, is seen to be dilated at the anterior extremity and obscurely divided by constrictions into the three primary vesicles of the brain.

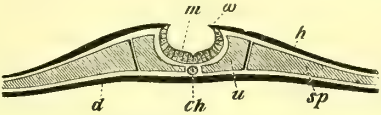


Fig. 411.—*Diagram of transverse section through an embryo before the closing-in of the medullary groove.* *m*, cells of epiblast lining the medullary groove which will form the spinal cord; *h*, epiblast; *d*, hypoblast; *ch*, noto-chord; *u*, protovertebra; *sp*, mesoblast; *w*, edge of lamina dorsalis, folding over medullary groove (Kölliker).

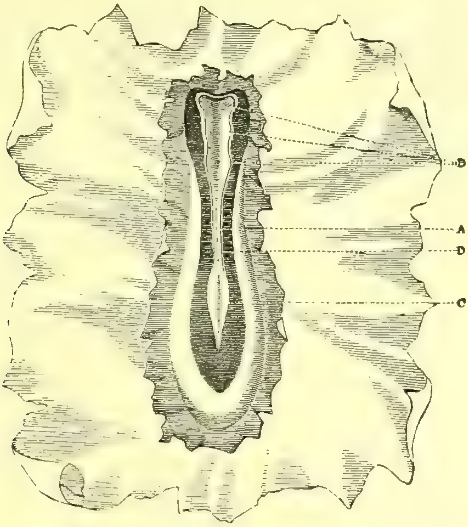


Fig. 412.—*Portion of the germinal membrane, with rudiments of the embryo; from the ovum of a bitch.* The primitive groove, A, is not yet closed, and at its upper or cephalic end presents three dilatations, B, which correspond to the three divisions or vesicles of the brain. At its lower extremity the groove presents a lancet-shaped dilatation (sinus rhomboidalis) C. The margins of the groove consist of clear pellucid nerve-substance. Along the bottom of the groove is observed a faint streak, which is probably the chorda dorsalis. D. Vertebral plates (Bischoff).

The part from which the spinal cord is formed is of nearly uniform calibre, while towards the posterior extremity is a lozenge-shaped dilatation, which is the last part to close in (fig. 412).

Notochord.—At the same time there appears in the middle line, immediately beneath the floor of the medullary groove, a rod-shaped structure formed by an aggregation of cells of the mesoblast; it soon becomes quite distinct from the remainder of the mesoblast, and constitutes an axial cord (notochord, *chorda dorsalis*) (*ch*, fig. 414) which extends nearly the whole length of the medullary canal, terminating anteriorly beneath the middle one of the three cerebral vesicles, and occupies the future position of the *bodies* of the vertebræ and basis cranii.

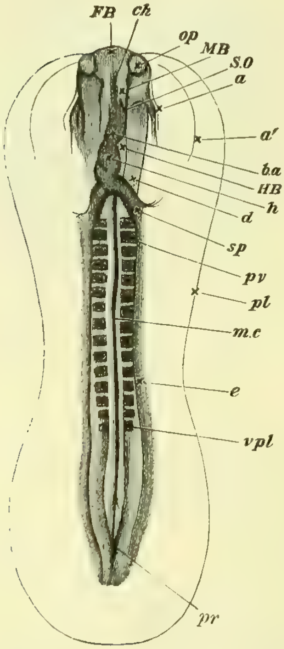


Fig. 413.—*Embryo chick* (36 hours), *viewed from beneath as a transparent object* (magnified). *pl*, outline of pellucid area; *FB*, fore-brain, or first cerebral vesicle: from its sides project *op*, the optic vesicles; *SO*, backward limit of somatopleure fold, "tucked in" under head; *a*, headfold of true amnion; *a′*, reflected layer of amnion, sometimes termed "false amnion;" *sp*, backward limit of splanchnopleure folds, along which run the omphalomesaraic veins uniting to form *h*, the heart, which is continued forwards into *ba*, the bulbus arteriosus; *d*, the fore-gut, lying behind the heart, and having a wide crescentic opening between the splanchnopleure folds; *HB*, hind-brain; *MB*, mid-brain; *pv*, protovertebræ lying behind the fore-gut; *mc*, line of junction of medullary folds and of notochord; *ch*, front end of notochord; *vpl*, vertebral plates; *pr*, the primitive groove at its caudal end (Foster and Balfour).

Protovertebræ.—Simultaneously on each side of the notochord appears a longitudinal thickening of the mesoblast.

Thus we have two lateral plates which when viewed from above are seen to be divided into a number of squarish segments (*protovertebræ*) by the formation of transverse clefts. The first three or four of these protovertebræ make their appearance in the cervical region, while one or two more are formed in front of this point: and the series is continued backward till the whole medullary canal is flanked by them (fig. 413).

Splitting of the Mesoblast.—External to the protovertebræ, the mesoblast now splits into two laminæ (*parietal* and *visceral*): of these the former, when traced out from the central axis, is seen to be in close apposition with the epiblast and gives origin to the parietes of the trunk, while the latter adheres more or less closely to the hypoblast, and gives rise to the serous and muscular walls of the alimentary canal and several other parts (fig. 414).

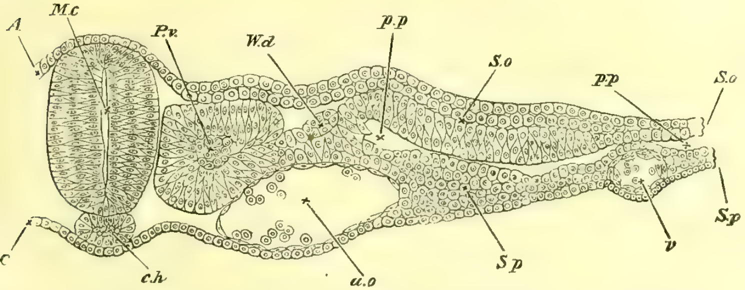


Fig. 414.—*Transverse section through dorsal region of embryo chick* (45 hrs.). One half of the section is represented: if completed it would extend as far to the left as to the right of the line of the medullary canal (*Mc*). *A*, epiblast; *C*, hypoblast, consisting of a single layer of flattened cells; *Mc*, medullary canal; *Pv*, protovertebra; *Wd*, Wolffian duct; *So*, somatopleure; *Sp*, splanchnopleure; *pp*, pleuro-peritoneal cavity; *ch*, notochord; *ao*, dorsal aorta, containing blood cells; *v*, blood-vessels of the yolk-sac (Foster and Balfour).

The united *parietal* layer of the mesoblast with the epiblast is termed *Somatopleure*, the united *visceral* layer and hypoblast, *Splanchnopleure.* The space between them is the pleuro-peritoneal cavity, which becomes subdivided by subsequent partitions into pericardium, pleura, and peritoneum.

Head and Tail Folds. Body Cavity.—Every vertebrate animal consists essentially of a longitudinal axis (vertebral column) with a neural canal above it, and a body-cavity (containing the alimentary canal) beneath.

We have seen how the earliest rudiments of the central axis and the neural canal are formed; we must now consider how the general body-cavity is developed. In the earliest stages the embryo lies flat on the surface of the yelk, and is not clearly marked off from the rest of the blastoderm: but gradually a crescentic depression (with its concavity backwards) is formed in the blastoderm, limiting the head of the embryo; the blastoderm is, as it were, tucked in under the head, which thus comes to project above the general surface of the membrane: a similar tucking in of blastoderm takes place at the caudal extremity, and thus the head and tail folds are formed (fig. 415).

Similar depressions mark off the embryo laterally, until it is completely surrounded by a sort of moat which it overhangs on all sides, and which clearly defines it from the yelk.

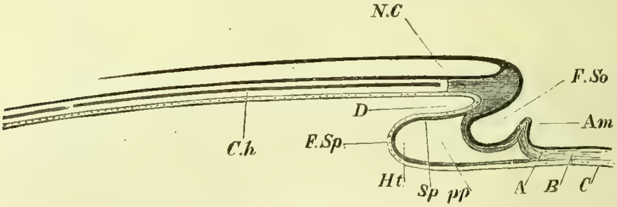


Fig. 415.—*Diagrammatic longitudinal section through the axis of an embryo.* The head-fold has commenced, but the tail-fold has not yet appeared. *FSo*, fold of the somatopleure; *FSp*, fold of the splanchnopleure; the line of reference, *FSo*, lies outside the embryo in the "moat," which marks off the overhanging head from the amnion; *D*, inside the embryo, is that part which is to become the fore-gut; *FSo* and *FSp*, are both parts of the head-fold, and travel to the left of the figure as development proceeds; *pp*, space between somatopleure and splanchnopleure, pleuro-peritoneal cavity; *Am*, commencing head-fold of amnion; *NC*, neural canal; *Ch.* notochord; *Ht*, heart; *A*, *B*, *C*, epiblast, mesoblast, hypoblast (Foster and Balfour).

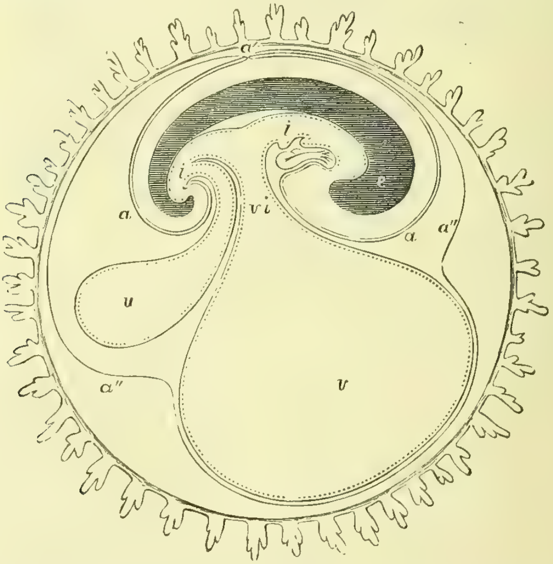


Fig. 416.—*Diagrammatic section showing the relation in a mammal between the primitive alimentary canal and the membranes of the ovum.* The stage represented in this diagram corresponds to that of the fifteenth or seventeenth day in the human embryo, previous to the expansion of the allantois: *c*, the villous chorion; *a*, the amnion; *a'*, the place of convergence of the amnion and reflexion of the false amnion *a'' a''*, or outer or corneous layer; *e*, the head and trunk of the embryo, comprising the primitive vertebræ and cerebro-spinal axis; *i*, *i*, the simple alimentary canal in its upper and lower portions. Immediately beneath the right hand *i* is seen the fœtal heart, lying in the anterior part of the pleuro-peritoneal cavity; *v*, the yolk-sac, or umbilical vesicle; *v i*, the vitello-intestinal opening; *u*, the allantois connected by a pedicle with the anal portion of the alimentary canal (From Quain's "Anatomy").

This moat runs in further and further all round beneath the overhanging embryo, till the latter comes to resemble a canoe turned upside-down, the ends and middle being, as it were, decked in by the folding or tucking in of the blastoderm, while on the ventral surface there is still a large communication with the yelk, corresponding to the "well" or undecked portion of the canoe.

This communication between the embryo and the yelk is gradually contracted by the further tucking in of the blastoderm from all sides, till it becomes narrowed down, as by an invisible constricting band, to a mere pedicle which passes out of the body of the embryo at the point of the future umbilicus.

Visceral Plates.—The downwardly folded portions of blastoderm are termed the *visceral plates.*

Thus we see that the body-cavity is formed by the downward folding of the visceral plates, just as the neural cavity is produced by the upward growth of the dorsal laminæ, the difference being that, in the visceral or ventral laminæ, all three layers of the blastoderm are concerned.

The folding in of the splanchnopleure, lined by hypoblast, pinches off, as it were, a portion of the yelk-sac, enclosing it in the body-cavity. This forms the rudiment of the alimentary canal, which at this period ends blindly towards the head and tail, while in the centre it communicates freely with the cavity of the yelk-sac through the canal termed *vitelline* or *omphalo-mesenteric duct.*

The yelk-sac thus becomes divided into two portions which communicate through the vitelline duct, that portion within the body giving rise, as above stated, to the digestive canal, and that outside the body remaining for some time as the *umbilical vesicle* (fig. 417, *ys*). The hypoblast forming the epithelium of the intestine is of course continuous with the lining membrane of the umbilical vesicle, while the visceral plate of the mesoblast is continuous with the outer layer of the umbilical vesicle.

All the above details will be clear on reference to the accompanying diagrams.

Fœtal Membranes.

Umbilical Vesicle or Yelk-sac.—The splanchnopleure, lined by hypoblast, forms the yelk-sac in Reptiles, Birds, and Mammals;

but in Amphibia and Fishes, since there is neither *amnion* nor *allantois*, the wall of the yelk-sac consists of all three layers of the blastoderm, enclosed, of course, by the original vitelline membrane.

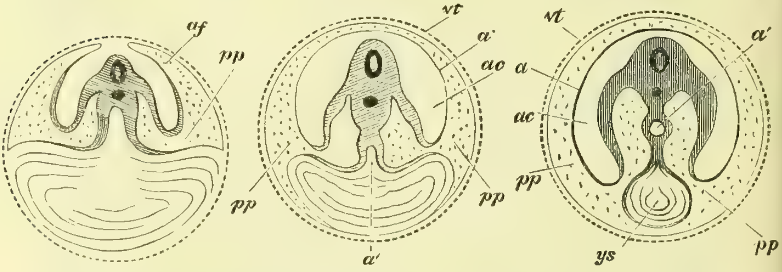


Fig. 417.—*Diagrams, showing three successive stages of development.* Transverse vertical sections. The yelk-sac, *ys*, is seen progressively diminishing in size. In the embryo itself the medullary canal and notochord are seen in section. *a′*, in middle figure, the alimentary canal, becoming pinched off, as it were, from the yelk-sac; *a′*, in right hand figure, alimentary canal completely closed; *a*, in last two figures, amnion; *ac*, cavity of amnion filled with amniotic fluid; *pp*, space between amnion and chorion, continuous with the pleuro-peritoneal cavity inside the body; *vt*, vitelline membrane; *ys*, yelk-sac, or umbilical vesicle (Foster and Balfour).

The body of the embryo becomes in great measure detached from the yelk-sac or umbilical vesicle, which contains, however, the greater part of the substance of the yelk, and furnishes a source whence nutriment is derived for the embryo. This nutriment is absorbed by the numerous vessels (omphalo-mesenteric) which ramify in the walls of the yelk-sac, forming what in birds is termed the *area vasculosa.* In Birds, the contents of the yelk-

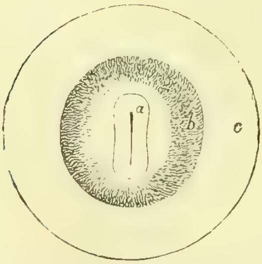


Fig. 418.—*Diagram showing vascular area in the chick.* *a*, area pellucida; *b*, area vasculosa; *c*, area vitellina.

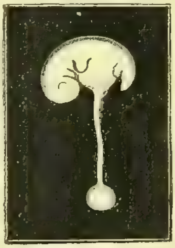


Fig. 419.—*Human embryo of fifth week with umbilical vesicle;* about natural size (Dalton). The human umbilical vesicle never exceeds the size of a small pea.

sac afford nourishment until the end of incubation, and the omphalo-mesenteric vessels are developed to a corresponding degree; but in Mammalia the office of the umbilical vesicle ceases at a very early period, the quantity of the yelk is small, and the embryo soon becomes independent of it by the connections it forms with the parent. Moreover, in Birds, as the sac is emptied, it is gradually drawn into the abdomen through the umbilical opening, which then closes over it: but in Mammalia it always remains on the outside; and as it is emptied it contracts (fig. 419), shrivels up, and together with the part of its duct external to the abdomen, is detached and disappears either before or at the termination of intra-uterine life, the period of its disappearance varying in different orders of Mammalia.

When blood-vessels begin to be developed, they ramify largely over the walls of the umbilical vesicle, and are actively concerned in absorbing its contents and conveying them away for the nutrition of the embryo.

The Amnion and Allantois.—At an early stage of development of the fœtus, and some time before the completion of the changes which have been just described, two important structures, called respectively the *amnion* and the *allantois*, begin to be formed.

Amnion.—The amnion is produced as follows:—Beyond the head- and tail-folds before described (p. 765), the somatopleure coated by epiblast, is raised into folds, which grow up, arching over the embryo, not only anteriorily and posteriorly but also laterally, and all converging towards one point over its dorsal surface (fig. 417). The growing up of these folds from all sides and their convergence towards one point very closely resembles the folding inwards of the visceral plates already described, and hence, by some, the point at which the amniotic folds meet over the back has been termed the "amniotic umbilicus."

The folds not only come into contact but coalesce. The inner of the two layers forms the *true amnion*, while the outer or reflected layer, sometimes termed the *false amnion*, coalesces with the inner surface of the original vitelline membrane to form the *chorion*. This growth of the amniotic folds must of course be clearly distinguished from the very similar process, already described, by which the walls of the neural canal are formed at a much earlier stage.

Amniotic Cavity.—The cavity between the true amnion and the external surface of the embryo becomes a closed space, termed the *amniotic cavity* (*ac*, fig. 417).

At first, the amnion closely invests the embryo, but it becomes gradually distended with fluid (liquor amnii), which, as pregnancy advances, reaches a considerable quantity.

This fluid consists of water containing small quantities of albumen and urea. Its chief function during gestation appears to be the mechanical one of affording equal support to the embryo on all sides, and of protecting it as far as possible from the effects of blows and other injuries to the abdomen of the mother.

The embryo up to the end of pregnancy is thus immersed in fluid, which during parturition serves the important purpose of gradually and evenly dilating the neck of the uterus to allow of the passage of the fœtus: when this is accomplished the amniotic sac bursts and the "waters" escape.

On referring to the diagrams (fig. 417), it will be obvious that the cavity outside the amnion (between it and the false amnion) is continuous with the pleuro-peritoneal cavity at the umbilicus. This cavity is not entirely obliterated even at birth, and contains a small quantity of fluid ("false waters"), which is discharged during parturition either before, or at the same time as the amniotic fluid.

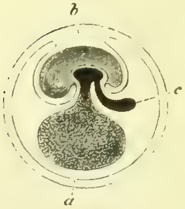


Fig. 420.—*Diagram of fecundated egg.* *a*, umbilical vesicle; *b*, amniotic cavity; *c*, allantois (Dalton).

Allantois.—Into the pleuro-peritoneal space the *allantois* sprouts out, its formation commencing during the development of the amnion.

Growing out from or near the hinder portion of the intestinal canal (*c*, fig. 420), with which it communicates, the allantois is at first a solid pear-shaped mass of splanchnopleure; but becoming vesicular by the projection into it of a hollow out-growth of hypoblast, and very soon simply membranous and vascular, it insinuates itself between the amniotic folds, just described, and comes into close contact and union with the outer of the two folds, which has itself, as before said, become one with the external investing membrane of the egg. As it grows, the allantois developes muscular tissue in its external wall and becomes exceedingly vascular; in birds (fig. 421) it envelopes the whole embryo—taking up vessels, so to speak, to the outer investing membrane of the egg, and lining the inner surface of the shell with a vascular membrane, by these means affording an extensive surface in which the blood may be aërated. In the human subject and in other Mammalia, the vessels carried out by the allantois are distributed only to a special part of the outer membrane or *chorion*, where, by interlacement with the vascular system of the mother, a structure called the *placenta* is developed.

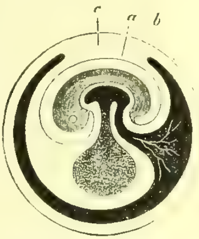
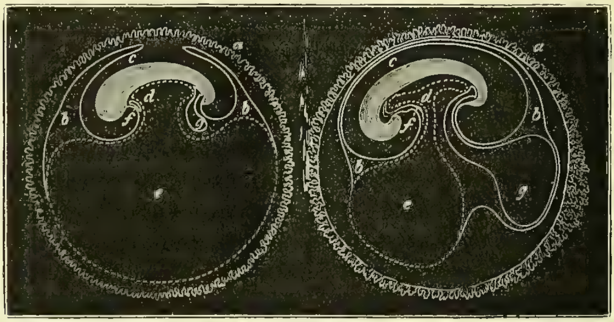


Fig. 421.—*Fecundated egg with allantois nearly complete.* *a*, inner layer of amniotic fold; *b*, outer layer of ditto; *c*, point where the amniotic folds come in contact. The allantois is seen penetrating between the outer and inner layers of the amniotic folds. This figure, which represents only the amniotic folds and the parts within them, should be compared with figs. 417, 423, in which will be found the structures external to these folds (Dalton).

In Mammalia, as the visceral laminæ close in the abdominal cavity, the allantois is thereby divided at the umbilicus into two portions; the outer part, extending from the umbilicus to the *chorion*, soon shrivelling; while the inner part, remaining in the abdomen, is in part converted into the urinary bladder; the portion of the inner part not so converted, extending from the bladder to the umbilicus, under the name of the *urachus*. After birth the umbilical cord, and with it the external and shrivelled portion of the allantois, are cast off at the umbilicus, while the *urachus* remains as an impervious cord stretched from the top of the urinary bladder to the umbilicus, in the middle line of the body, immediately beneath the parietal layer of the peritoneum. It is sometimes enumerated among the ligaments of the bladder.

It must not be supposed that the phenomena which have been successively described, occur in any regular order one after another. On the contrary, the development of one part is going on side by side with that of another.

The Chorion.—It has been already remarked that the *allantois* is a structure which extends from the body of the fœtus to the outer investing membrane of the ovum, that it insinuates itself between the two layers of the amniotic fold, and becomes fused with the outer layer, which has itself become previously fused with the vitelline membrane. By these means the external investing membrane of the ovum, or the *chorion*, as it is now called, represents three layers, namely, the original vitelline membrane, the outer layer of the amniotic fold, and the allantois.



Figs. 422 and 423 (after Todd and Bowman). *a*, chorion with villi. The villi are shown to be best developed in the part of the chorion to which the allantois is extending; this portion ultimately becomes the placenta; *b*, space between the two layers of the amnion; *c*, amniotic cavity; *d*, situation of the intestine, showing its connection with the umbilical vesicle; *e*, umbilical vesicle; *f*, situation of heart and vessels; *g* allantois.

Very soon after the entrance of the ovum into the uterus, in the human subject, the outer surface of the chorion is found beset with fine processes, the so-called *villi of the chorion* (*a*, figs. 422, 423), which give it a rough and shaggy appearance. At first only cellular in structure, these little outgrowths subsequently become vascular by the development in them of loops of capillaries (fig. 423); and the latter at length form the minute extremities of the blood-vessels which are, so to speak, conducted from the fœtus to the chorion by the allantois. The function of the villi of the chorion is evidently the absorption of nutrient matter for the fœtus; and this is probably supplied to them at first from the fluid matter, secreted by the follicular glands of the uterus, in which they are soaked. Soon, however, the fœtal

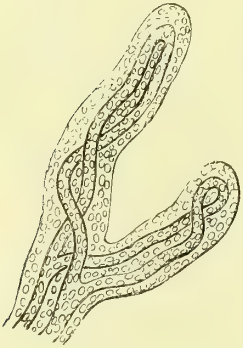


Fig. 424.

vessels of the villi come into more intimate relation with the vessels of the uterus. The part at which this relation between the vessels of the fœtus and those of the parent ensues, is not, however, over the whole surface of the chorion: for, although all the villi become vascular, yet they become indistinct or disappear except at one part where they are greatly developed, and by their branching give rise, with the vessels of the uterus, to the formation of the *placenta.*

To understand the manner in which the *fœtal* and *maternal* blood-vessels come into relation with each other in the placenta, it is necessary briefly to notice the changes which the uterus undergoes after impregnation. These changes consist especially of alterations in structure of the superficial part of the mucous membrane which lines the interior of the uterus, and which forms, after a kind of development to be immediately described, the *membrana decidua,* so called on account of its being discharged from the uterus at birth.

Formation of the Placenta.

The mucous membrane of the human uterus, which consists of a matrix of connective tissue containing numerous corpuscles (adenoid tissue), and is lined internally by columnar ciliated epithelium, is abundantly beset with tubular glands, arranged perpendicularly to the surface (fig. 425). These follicles are very small in the unimpregnated uterus; but when examined shortly after impregnation, they are found elongated, enlarged, and much waved and contorted towards their deep and closed extremity,

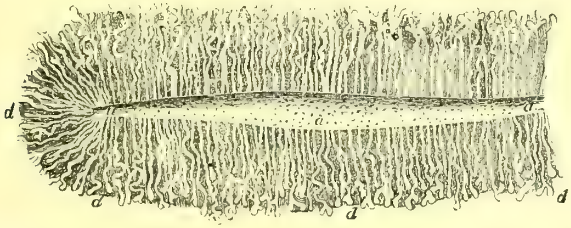


Fig. 425.—*Section of the lining membrane of a human uterus at the period of commencing pregnancy* showing the arrangement and other peculiarities of the glands, *d, d, d,* with their orifices, *a, a, a,* on the internal surface of the organ. Twice the natural size.

which is implanted at some depth in the tissue of the uterus, and may dilate into two or three closed sacculi (fig. 425).

The glands are lined by columnar ciliated epithelium, and they open on the inner surface of the mucous membrane by small round orifices set closely together (*a*, *a*, fig. 426).

On the internal surface of the mucous membrane may be seen the circular orifices of the glands, many of which are, in the early period of pregnancy, surrounded by a whitish ring, formed of the epithelium which lines the follicles (fig. 426).

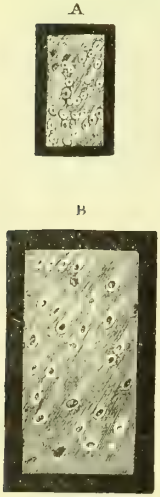


Fig. 426.—*Two thin segments of human decidua after recent impregnation*, viewed on a dark ground: they show the openings on the surface of the membrane. A is magnified six diameters, and B twelve diameters. At 1, the lining of epithelium is seen within the orifices, at 2 it has escaped (Sharpey).

Membrana decidua.—Coincidently with the occurrence of pregnancy, important changes occur in the structure of the mucous membrane of the uterus. The epithelium and sub-epithelial connective tissue, together with the tubular glands, increase rapidly, and there is a greatly increased vascularity of the whole mucous membrane, the vessels of the mucous membrane becoming larger and more numerous; while a substance composed chiefly of nucleated cells fills up the interfollicular spaces in which the blood-vessels are contained. The effect of these changes is an increased thickness, softness, and vascularity of the mucous membrane, the superficial part of which itself forms the *membrana decidua.*

The object of this increased development seems to be the production of nutritive materials for the ovum; for the cavity of the uterus shortly becomes filled with secreted fluid, consisting almost entirely of nucleated cells in which the villi of the chorion are imbedded.

When the ovum first enters the uterus it becomes imbedded in the structure of the decidua, which is yet quite soft, and in which soon afterwards three portions are distinguishable. These have been named the decidua *vera*, the decidua *reflexa*, and the decidua *serotina*. The first of these, the decidua *vera*, lines the cavity of the uterus ; the second, or decidua *reflexa*, is a part of the decidua vera which grows up around the ovum, and, wrapping it closely, forms its immediate investment.

The third, or decidua *serotina*, is the part of the decidua vera which becomes especially developed in connection with those vill of the chorion, which, instead of disappearing, remain to form the fœtal part of the *placenta*.

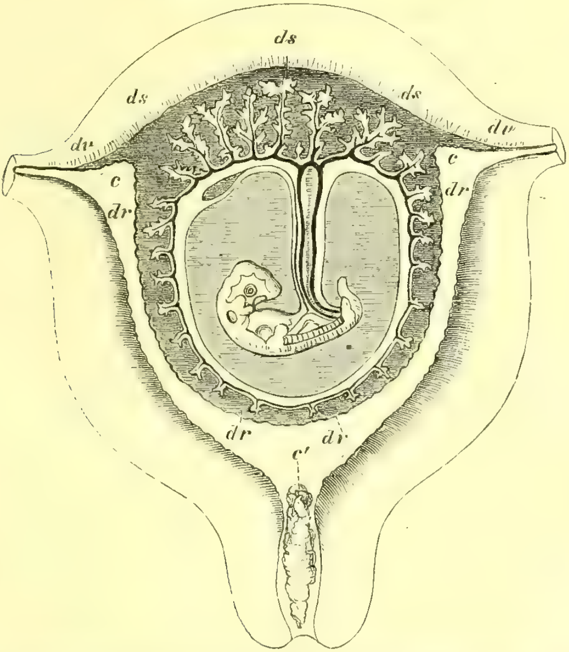


Fig. 427.—*Diagrammatic view of a vertical transverse section of the uterus at the seventh or eighth week of pregnancy.* c, c, c′, cavity of uterus, which becomes the cavity of the decidua, opening at *c*, *c*, the cornua, into the Fallopian tubes, and at *c*′ into the cavity of the cervix, which is closed by a plug of mucus; *d v*, decidua vera; *d r*, decidua reflexa, with the sparser villi imbedded in its substance; *d s*, decidua serotina, involving the more developed chorionic villi of the commencing placenta. The fœtus is seen lying in the amniotic sac; passing up from the umbilicus is seen the umbilical cord and its vessels, passing to their distribution in the villi of the chorion; also the pedicle of the yelk sac, which lies in the cavity between the amnion and chorion (Allen Thomson).

In connection with these villous *processes* of the chorion, there are developed *depressions* or *crypts* in the decidual mucous membrane, which correspond in shape with the villi they are to lodge ; and thus the chorionic villi become more or less imbedded in the maternal structures. These uterine crypts, it is important to note, are not, as was once supposed, merely the open mouths of the uterine follicles (Turner).

As the ovum increases in size, the decidua vera and the decidua reflexa gradually come into contact, and in the third month of pregnancy the cavity between them has quite disappeared. Henceforth it is very difficult, or even impossible, to distinguish the two layers.

The Placenta.—During these changes the deeper part of the mucous membrane of the uterus, at and near the region where the placenta is placed, becomes hollowed out by sinuses, or cavernous spaces, which communicate on the one hand with arteries and on the other with veins of the uterus. Into these sinuses the villi of the chorion protrude, pushing the thin wall of the sinus before them, and so come into intimate relation with the blood contained in them. There is no direct communication between the blood-vessels of the mother and those of the fœtus; but the layer or layers of membrane intervening between the blood of the one and of the other offer no obstacle to a free interchange of matters between them. Thus the villi of the chorion containing fœtal blood, are bathed or soaked in maternal blood contained in the uterine sinuses. The arrangement may be roughly compared to filling a glove with fœtal blood, and dipping its fingers into a vessel containing maternal blood. But in the fœtal villi there is a constant stream of blood into and out of the loop of capillary blood-vessels contained in it, as there is also into and out of the maternal sinuses.

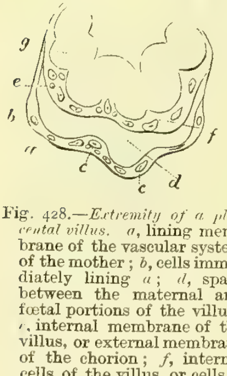


Fig. 428.—*Extremity of a placental villus.* *a*, lining membrane of the vascular system of the mother; *b*, cells immediately lining *a*; *d*, space between the maternal and fœtal portions of the villus; *e*, internal membrane of the villus, or external membrane of the chorion; *f*, internal cells of the villus, or cells of the chorion; *g*, loop of umbilical vessels (Goodsir).

It would seem from the observations of Goodsir, that, at the villi of the placental tufts, where the fœtal and maternal portions of the placenta are brought into close relation with each other, the blood in the vessels of the mother is separated from that in the vessels of the fœtus by the intervention of two distinct sets of nucleated cells (fig. 428). One of these (*b*) belongs to the maternal portion of the placenta, is placed between the membrane of the villus and that of the vascular system of the mother, and is probably designed to separate from the blood of the parent the materials destined for the blood of the fœtus; the other (*f*) belongs to the fœtal portion of the placenta, is situated between the membrane of the villus and the loop of vessels contained within, and probably serves for the absorption of the material secreted by the other sets of cells, and for its conveyance into the blood-vessels of the fœtus. Between the two sets of cells with their investing membrane there exists a space (*d*), into which it is probable that the materials secreted by the one set of cells of the villus are poured in order that they may be absorbed by the other set, and thus conveyed into the fœtal vessels.

Not only, however, is there a passage of materials from the blood of the mother into that of the fœtus, but there is a mutual interchange of materials between the blood both of fœtus and of parent; the latter supplying the former with nutriment, and in turn abstracting from it materials which require to be removed

Alexander Harvey's experiments were very decisive on this point. The view has also received abundant support from Hutchinson's important observations on the communication of syphilis from the father to the mother, through the instrumentality of the fœtus; and still more from Savory's experimental researches, which prove quite clearly that the female parent may be directly inoculated through the fœtus. Having opened the abdomen and uterus of a pregnant bitch, Savory injected a solution of strychnia into the abdominal cavity of one fœtus, and into the throracic cavity of another, and then replaced all the parts, every precaution being taken to prevent escape of the poison. In less than half an hour the bitch died from tetanic spasms: the fœtuses operated on were also found dead, while the others were alive and active. The experiments, repeated on other animals with like results, leave no doubt of the rapid and direct transmission of matter from the fœtus to the mother, through the blood of the placenta.

The placenta, therefore, of the human subject is composed of a *fœtal* part and a *maternal* part,—the term placenta properly including all that entanglement of fœtal villi and maternal sinuses, by means of which the blood of the fœtus is enriched and purified after the fashion necessary for the proper growth and development of those parts which it is designed to nourish.

The importance of the placenta is at once apparent if we remember that during the greater portion of intra-uterine life the maternal blood circulating in its vessels supplies the fœtus with both food and oxygen. It thus performs the functions which in later life are discharged by the alimentary canal and lungs.

The whole of this structure is not, as might be imagined, thrown off immediately after birth. The greater part, indeed, comes away at that time, as the *after-birth*: and the separation of this portion takes place by a rending or crushing through of that part at which its cohesion is least strong, namely, where it is most burrowed and undermined by the cavernous spaces before referred to. In this way it is cast off with the fœtal membrane and the decidua *vera* and *reflexa*, together with a part of the decidua *serotina*. The remaining portion withers, and disappears by being gradually either absorbed, or thrown off in the uterine discharges or the *lochia*, which occur at this period.

A new mucous membrane is of course gradually developed, as the old one, by its peculiar transformation into what is called the decidua, ceases to perform its original functions.

The *umbilical cord*, which in the latter part of fœtal life is almost solely composed of the two arteries and the single vein which respectively convey fœtal blood to and from the placenta, contains the remnants of other structures which in the early stages of the development of the embryo were, as already related, of great comparative importance. Thus, in early fœtal life, it is composed of the following parts:—(1.) Externally, a layer of the amnion, reflected over it from the umbilicus. (2.) The umbilical vesicle with its duct and appertaining omphalo-mesenteric blood-vessels. (3.) The remains of the allantois, and continuous with it the urachus. (4.) The umbilical vessels, which, as just remarked, ultimately form the greater part of the cord.

Development of Organs.

It remains now to consider in succession the development of the several organs and systems of organs in the further progress of the embryo. The accompanying figure (fig. 429) shows the chief organs of the body in a moderately early stage of development.

Development of the Vertebral Column and Cranium.

The primitive part of the vertebral column in all the Vertebrata is the *chorda dorsalis* (notochord), which consists entirely of soft cellular cartilage. This cord tapers to a point at the cranial and caudal extremities of the animal. In the progress of its development, it is found to become enclosed in a membranous sheath, which at length acquires a fibrous structure, composed of transverse annular fibres. The chorda dorsalis is to be regarded as the azygos axis of the spinal column, and, in particular, of the future bodies of the vertebræ, although it never itself passes into the state of hyaline cartilage or bone, but remains enclosed as in a case within the persistent parts of the vertebral column which are developed around it. It is permanent, however, only in a few animals: in the majority only traces of it persist in the adult animal.

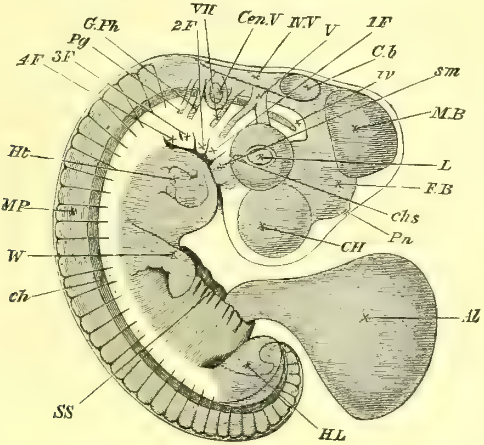


Fig. 429.—*Embryo chick* (4th day), *viewed as a transparent object*, lying on its left side (magnified). *C H*, cerebral hemispheres; *F B*, fore-brain or vesicle of third ventricle, with *P n*, pineal gland projecting from its summit; *M B*, mid-brain; *C b*, cerebellum; *IV V*, fourth ventricle; *L*, lens; *c h s*, choroidal slit; *Cen V*, auditory vesicle; *s m*, superior maxillary process; 1*F*, 2*F*, &c., first, second, third, and fourth visceral folds; *V*, fifth nerve, sending one branch (ophthalmic) to the eye, and another to the first visceral arch; *VII*, seventh nerve, passing to the second visceral arch; *G Ph*, glossopharyngeal nerve, passing to the third visceral arch; *P g*, pneumogastric nerve, passing towards the fourth visceral arch; *i v*, investing mass; *c h*, notochord; its front end cannot be seen in the living embryo, and it does not end as shown in the figure, but takes a sudden bend downwards, and then terminates in a point; *H t*, heart seen through the walls of the chest; *M P*, muscle-plates; *W*, wing, showing commencing differentiation of segments, corresponding to arm, forearm, and hand; *H L*, hind-limb, as yet a shapeless bud, showing no differentiation. Beneath it is seen the curved tail (Foster and Balfour).

In many Fish no true vertebræ are developed, and there is every gradation from the *amphioxus*, in which the notochord persists through life and there are no vertebral segments, through the lampreys in which there are a few scattered cartilaginous segments, and the sharks, in which many of the vertebræ are partly ossified, to the bony fishes, such as the cod and herring, in which the vertebral column consists of a number of distinct ossified vertebræ, with remnants of the notochord between them. In Amphibia, Reptiles, Birds, and Mammals, there are distinct vertebræ, which are formed as follows :—

Protovertebræ.—The *protovertebræ*, which have been already mentioned (p. 764), send processes downwards and inwards to surround the notochord, and also upwards between the medullary canal and the epiblast covering it. In the former situation, the cartilaginous bodies of the vertebræ make their appearance, in the latter their arches, which enclose the neural canal.

The vertebræ do not exactly correspond in their position with the protovertebræ : but each permanent vertebra is developed from the contiguous halves of two protovertebræ. The original segmentation of the protovertebræ disappears and a fresh subdivision occurs in such a way that a permanent invertebral disc is developed opposite the centre of each protovertebra. Meanwhile the protovertebræ split into a dorsal and ventral portion. The former is termed the *musculo-cutaneous* plate, and from it are developed all the muscles of the back together with the cutis of the dorsal region (the epidermis being derived from the epiblast). The ventral portions of the protovertebræ, as we have already seen, give rise to the vertebræ and heads of the ribs, but the outer part of each also gives rise to a spinal ganglion and nerve-root.

The chorda is now enclosed in a case, formed by the bodies of the vertebræ, but it gradually wastes and disappears. Before the disappearance of the chorda, the ossification of the bodies and arches of the vertebræ begins at distinct points.

The ossification of the body of a vertebra is first observed at the point where the two primitive elements of the vertebræ have united inferiorly. Those vertebræ which do not bear ribs, such as the cervical vertebræ, have generally an additional centre of ossification in the transverse process, which is to be regarded as an abortive rudiment of a rib. In the fœtal bird, these additional ossified portions exist in all the cervical vertebræ, and gradually become so much developed in the lower part of the cervical region as to form the upper false ribs of this class of animals. The same parts exist in mammalia and man ; those of the last cervical vertebræ are the most developed, and in children may, for a considerable period be distinguished as a separate part on each side, like the root or head of a rib.

The true cranium is a prolongation of the vertebral column, and is developed at a much earlier period than the facial bones. Originally, it is formed of but one mass, a cerebral capsule, the chorda dorsalis being continued into its base, and ending there with a tapering point. At an early period the head is bent downwards and forwards round the end of the chorda dorsalis in such a way that the *middle* cerebral vesicle, and not the anterior, comes to occupy the highest position in the head.

Pituitary Body.—In connection with this must be mentioned the development of the pituitary body. It is formed by the meeting of two out-growths, one from the fœtal brain, which grows downwards, and the other from the epiblast of the buccal cavity, which grows up towards it. The surrounding mesoblast also takes part in its formation. The connection of the first process with the brain becomes narrowed, and persists as the infundibulum, while that of the other process with the buccal cavity disappears completely at a spot corresponding with the future position of the body of the sphenoid.

The first appearance of a solid support at the base of the cranium observed by Müller in fish, consists of two elongated bands of cartilage (trabeculæ cranii), one on the right and the other on the left side, which are connected with the cartilaginous capsule of the auditory apparatus, and which diverge to enclose the pituitary body, uniting in front to form the septum nasi beneath the anterior end of the cerebral capsule. Hence, in the cranium, as in the spinal column, there are at first developed at the sides of the chorda dorsalis two symmetrical elements, which subsequently coalesce, and may wholly enclose the chorda.

The brain-case consists of three segments: occipital, parietal, and frontal, corresponding in their relative position to the three primitive cerebral vesicles; it may also be noted that in front of each segment is developd a sense-organ (auditory, ocular, and olfactory, from behind forwards). The basis cranii consists at an early period of an unsegmented cartilaginous rod, developed round the notochord, and continued forward beyond its termination into the *trabeculæ cranii*, which bound the pituitary fossa on either side

In this cartilaginous rod three centres of ossification appear:

basi-occipital, basi-sphenoid, and pre-sphenoid, one corresponding to each segment.

The bones forming the vault of the skull (frontal, parietal, squamous portion of temporal), with the exception of the squamo-occipital, which is preformed in cartilage, are ossified in membrane.

Development of the Face and Visceral Arches.

It has been said before that at an early period of development of the embryo, there grow up on the sides of the primitive groove the so-called *dorsal laminæ*, which at length coalesce, and complete by their union the spinal canal. The same process essentially takes place in the head, so as to enclose the cranial cavity.

Visceral laminæ.—The so-called *visceral laminæ* have been also described as passing forwards, and gradually coalescing in front, as the dorsal laminæ do behind, and thus enclosing the thoracic and abdominal cavity. An analogous process occurs in the facial and cervical regions, but the enclosing laminæ, instead of being simple, as in the former instances, are cleft.

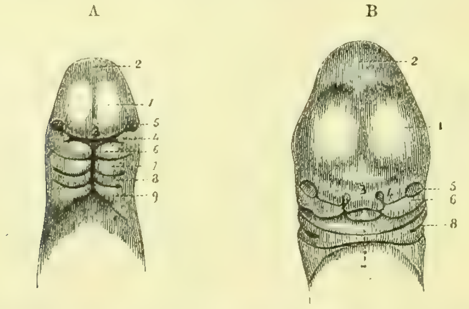


Fig. 430.—A. *Magnified view from before of the head and neck of a human embryo of about three weeks* (from Ecker).—1, anterior cerebral vesicle or cerebrum; 2, middle ditto; 3, middle or fronto-nasal process; 4, superior maxillary process; 5, eye; 6, inferior maxillary process, or first visceral arch, and below it the first cleft; 7, 8, 9, second, third, and fourth arches and clefts. B. Anterior view of the head of a human fœtus of about the fifth week (from Ecker, as before, fig. IV.). 1, 2, 3, 5, the same parts as in A; 4, the external nasal or lateral frontal process; 6, the superior maxillary process; 7, the lower jaw; ×, the tongue; 8, first branchial cleft becoming the meatus auditorius externus.

In this way the so-called visceral *arches* and *clefts* are formed, four on each side (fig. 430, A.).

From or in connection with these arches the following parts are developed:—

The first arch (mandibular) contains a cartilaginous rod (Meckel's cartilage), around the distal end of which the lower jaw is developed, while the malleus is ossified from the proximal end.

From near the root of this arch the maxillary process grows forwards and inwards towards the middle line; from it are formed the superior maxillary and malar bones. A pair of cartilaginous rods (pterygo-palatine), parallel to the trabeculæ cranii, give origin to the external pterygoid plate of the sphenoid and the palate bones.

The cleft between the maxillary process and the mandibular (or first visceral arch) forms the mouth.

When the maxillary processes on the two sides fail partially or completely to unite in the middle line, the well-known condition termed *cleft palate* results. When the integument of the face presents a similar deficiency, we have the deformity known as *hare-lip*. Though these two deformities frequently co-exist, they are by no means always necessarily associated.

The upper part of the face in the middle line is developed from the so-called *frontal-nasal* process (A, 3, fig. 430). From the *second* arch are developed the *incus*, *stapes*, and *stapedius* muscle, the styloid process of the *temporal* bone, the *stylo-hyoid* ligament, and the *smaller cornu* of the *hyoid* bone. From the *third* visceral arch, the *greater cornu* and *body* of the hyoid bone. In man and other mammalia the *fourth* visceral arch is indistinct. It occupies the position where the neck is afterwards developed.

A distinct connection is traceable between these visceral arches and certain cranial nerves: the trigeminal, the facial, the glossopharyngeal, and the pneumogastric. The ophthalmic division of the trigeminal supplies the trabecular arch; the superior and

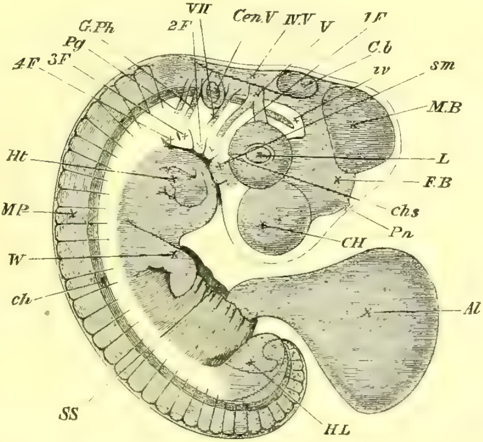


Fig. 431.—For description see fig. 429.

inferior maxillary divisions supply the maxillary and mandibular arches respectively.

The facial nerve distributes one branch (chorda tympani) to the first visceral arch, and others to the second visceral arch. Thus it divides, enclosing the first visceral cleft.

Similarly, the glosso-pharyngeal divides to enclose the second visceral cleft, its lingual branch being distributed to the second, and its pharyngeal branch to the third arch.

The vagus, too, sends a branch (pharyngeal) along the third arch, and in fishes it gives off paired branches, which divide to enclose several successive branchial clefts.

Development of the Extremities.

The extremities are developed in an uniform manner in all vertebrate animals. They appear in the form of leaf-like elevations from the parieties of the trunk (see fig. 432), at points where more or less of an arch will be produced for them within. The primitive form of the extremity is nearly the same in all Vertebrata, whether it be destined for swimming, crawling, walking, or flying. In the human fœtus the fingers are at first united, as if webbed for swimming; but this is to be regarded not so much as an approximation

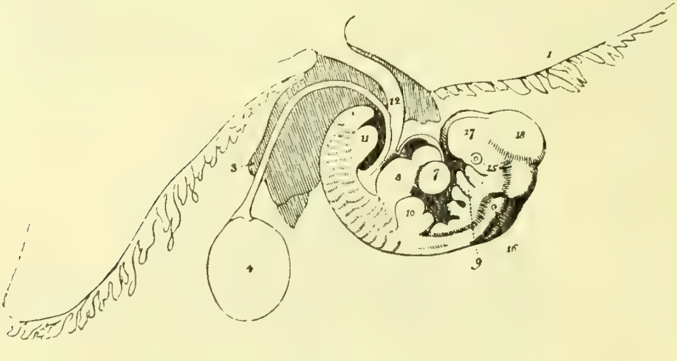


Fig. 432.—*A human embryo of the fourth week, 3½ lines in length.*—1, the chorion; 3, part of the amnion; 4, umbilical vesicle with its long pedicle passing into the abdomen; 7, the heart; 8, the liver; 9, the visceral arch destined to form the lower jaw, beneath which are two other visceral arches separated by the branchial clefts; 10, rudiment of the upper extremity; 11, that of the lower extremity; 12, the umbilical cord; 15, the eye; 16, the ear; 17, cerebral hemispheres; 18, optic lobes, corpora quadrigemina (Müller).

to the form of aquatic animals, as the primitive form of the hand, the individual parts of which subsequently become more completely isolated.

The fore-limb always appears before the hind-limb and for some time continues in a more advanced state of development. In both limbs alike, the distal segment (hand or foot) is separated by a slight notch from the proximal part of the limb, and this part is subsequently divided again by a second notch (knee or elbow-joint).

Development of the Vascular System.

At an early stage in the development of the embryo-chick, the so-called "area vasculosa" begins to make its appearance. A number of branched cells in the mesoblast send out processes which unite so as to form a network of protoplasm with nuclei at the nodal points. A large number of the nuclei acquire a red colour; these form the red blood-cells. The proto-plasmic processes become hollowed out in the centre so as to form a closed system of branching canals, in the walls of which the rest of the nuclei remain imbedded. In the blood-vessels thus formed, the circulation of the embryonic blood commences.

According to Klein's researches, the first blood-vessels in the chick are developed from embryonic cells of the mesoblast, which swell up and become vacuolated, while their nuclei undergo segmentation. These cells send out protoplasmic processes, which unite with corresponding ones from other cells, and become hollowed, give rise to the capillary wall composed of endothelial cells; the blood corpuscles being budded off from the endothelial wall by a process of gemmation.

Heart.—About the same time the heart makes its appearance as a solid mass of cells of the splanchnopleure.

At this period the anterior part of the alimentary tube ends blindly beneath the notochord. It is beneath the posterior end of this "fore-gut" (as it may be termed) that the heart begins to be developed. A cavity is hollowed out longitudinally in the mass of cells; the central cells float freely in the fluid, which soon begins to circulate by means of the rhythmic pulsations of the embryonic heart.

These pulsations take place even before the appearance of a cavity, and immediately after the first "laying down" of the cells from which the heart is formed, and long before muscular fibres or ganglia have been formed in the cardiac walls. At first they seldom exceed from fifteen to eighteen in the minute. The fluid within the cavity of the heart shortly assumes the characters of blood. At the same time the cavity itself forms a communication with the great vessels in contact with it, and the cells of which its walls are composed are transformed into fibrous and muscular tissues, and into epithelium. In the developing chick it can be observed with the naked eye as a minute red pulsating point before the end of the second day of incubation.

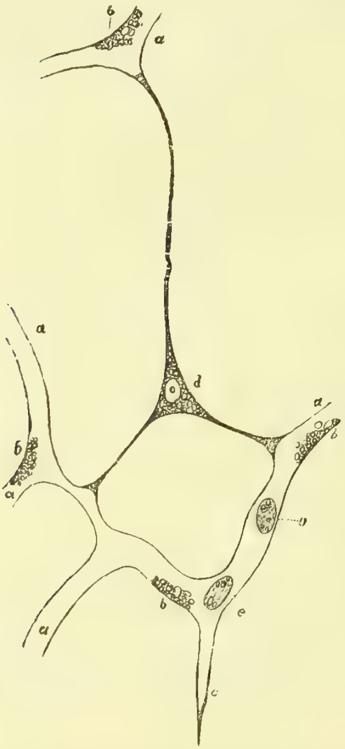


Fig. 433.—*Capillary blood-vessels of the tail of a young larval frog.* *a*, capillaries permeable to blood; *b*, fat-granules attached to the walls of the vessels, and concealing the nuclei; *c*, hollow prolongation of a capillary, ending in a point; *d*, a branching cell with nucleus and fat-granules; it communicates by three branches with prolongation of capillaries already formed; *e*, *e*, blood corpuscles still containing granules of fat. × 350 times (Kölliker).

Blood-vessels.—Blood-vessels appear to be developed in two ways, according to the size of the vessels. In the formation of large blood-vessels, masses of embryonic cells similar to those from which the heart and other structures of the embryo are developed, arrange themselves in the position, form, and thickness of the developing vessel. Shortly afterwards the cells in the interior of a column of this kind seem to be developed into blood-corpuscles, while the external layer of cells is converted into the walls of the vessel.

Capillaries.—In the development of capillaries another plan is pursued. This has been well illustrated by Kölliker, as observed in the tails of tadpoles. The first lateral vessels of the tail have the form of simple arches, passing between the main artery and vein, and are produced by the junction of prolongations, sent from both the artery and vein, with certain elongated or star-shaped cells, in the substance of the tail. When these arches are formed and are permeable to blood, new prolongations pass from them, join other radiated cells, and thus form secondary arches (fig. 434). In this manner, the capillary network extends in proportion as the tail increases in length and breadth, and it, at the same time, becomes more dense by the formation, according to the same plan, of fresh vessels within its meshes. The prolongations by which the vessels communicate with the star-shaped cells, consist at first of narrow pointed projections from the side of the vessels, which gradually elongate until they come in contact with the radiated processes of the cells. The thickness of such a prolongation often does not exceed that of a fibril of fibrous tissue, and at first it is perfectly solid; but, by degrees, especially after its junction with a cell, or with another prolongation, or with a vessel already permeable to blood, it enlarges, and a cavity then forms in its interior (see figs. 434, 435). This

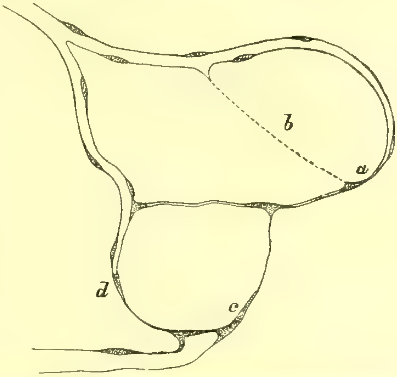


Fig. 434.—*Development of capillaries in the regenerating tail of a tadpole.* *a, b, c, d,* sprouts and cords of protoplasm (Arnold).

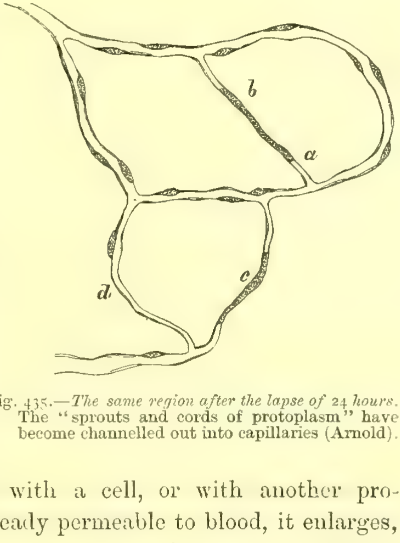


Fig. 435.—*The same region after the lapse of 24 hours.* The "sprouts and cords of protoplasm" have become channelled out into capillaries (Arnold).

tissue is well calculated to illustrate the various steps in the development of blood-vessels from elongating and branching cells.

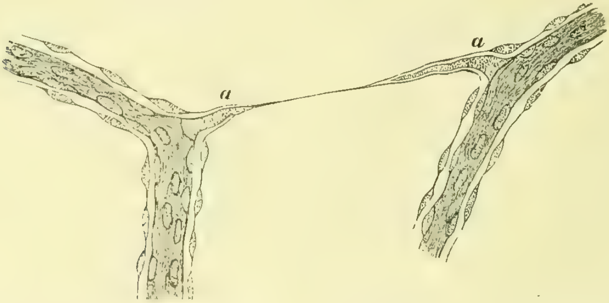


Fig. 436—*Capillaries from the vitreous humour of a fœtal calf.* Two vessels are seen connected by a "cord" of protoplasm, and clothed with an adventitia, containing numerous nuclei. *a*, insertion of this "cord" into the primary walls of the vessels. (Frey.)

In many cases a whole network of capillaries is developed from a network of branched, embryonic connective-tissue corpuscles by the joining of their processes, the multiplication of their nuclei, and the vacuolation of the cell-substance. The vacuoles gradually coalesce till all the partitions are broken down and the originally solid protoplasmic cell-substance is, so to speak, tunnelled out into a number of tubes.

Capillaries may also be developed from cells which are originally spheroidal, vacuoles form in the interior of the cells gradually becoming united by fine protoplasmic processes: by the extension of the vacuoles into them, capillary tubes are gradually formed.

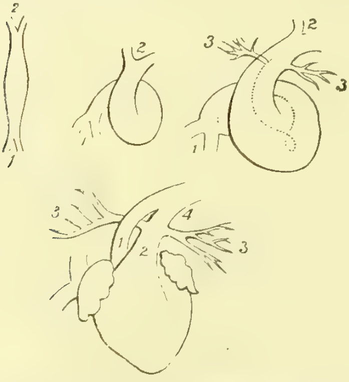


Fig. 437.—*Fœtal heart in successive stages of development.* 1, venous extremity; 2, arterial extremity; 3, 3, pulmonary branches; 4, ductus arteriosus. (Dalton.)

Morphology. **Heart.**—When it first appears, the heart is approximately tubular in form. It receives at its two posterior angles the two omphalo-mesenteric veins, and gives off anteriorly the primitive aorta (fig. 437).

It soon, however, becomes curved somewhat in the shape of a horse-shoe, with the convexity towards the right, the venous end being at the same time drawn up towards the head, so that it finally lies behind and somewhat to the right of the arterial. It also becomes partly divided by constrictions into three cavities.

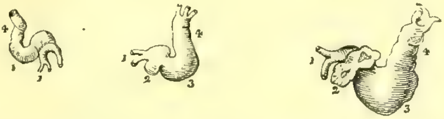


Fig. 438.—*Heart of the chick at the 45th, 65th, and 85th hours of incubation.* 1, the venous trunks; 2, the auricle; 3, the ventricle; 4, the bulbus arteriosus. (Allen Thomson.)

Of these three cavities which are developed in all Vertebrata, that at the venous end is the simple auricle, that at the arterial end the bulbous arteriosus, and the middle one is the simple ventricle.

These three parts of the heart contract in succession. The auricle and the bulbus arteriosus at this period lie at the extremities of the horse-shoe. The bulging out of the middle portion inferiorly gives the first indication of the future form of the ventricle (fig. 438). The great curvature of the horse-shoe by the same means becomes much more developed than the smaller curvature between the auricle and bulbus; and the two extremities, the auricle and bulb, approach each other superiorly, so as to produce a greater resemblance to the later form of the heart, whilst the ventricle becomes more and more developed inferiorly. The heart of Fishes retains these three cavities, no further division by internal septa into right and left chambers taking place. In Amphibia, also, the heart throughout life consists of the three muscular divisions which are so early formed in the embryo; but the auricle is divided internally by a septum into a pulmonary and systemic auricle. In Reptiles, not merely the auricle is thus divided into two cavities, but a similar septum is more or less developed in the ventricle. In Birds and Mammals, both auricle and ventricle undergo complete division by septa; whilst in these animals as well as in reptiles, the bulbus aortæ is not permanent, but becomes lost in the ventricles. The septum dividing the ventricle commences at the apex and extends upwards. The subdivision of the auricles is very early foreshadowed by the outgrowth of the two auricular appendages, which occurs before any septum is formed externally. The septum of the auricles is developed from a semilunar fold, which extends from above downwards. In man, the septum between the ventricles, according to Meckel, begins to be formed about the fourth week, and at the end of eight weeks is complete. The septum of the auricles, in man and all animals which possess it, remains imperfect throughout fœtal life. When the partition of the auricles is first commencing, the two venæ cavæ have different relations to the two cavities. The superior cava enters, as in the adult, into the right auricle; but the inferior cava is so placed that it appears to enter the left auricle, and the posterior part of the septum of the auricles is formed by the Eustachian valve, which extends from the point of entrance of the inferior cava. Subsequently, however, the septum, growing from the anterior wall close to the upper end of the ventricular septum, becomes directed more and more to the left of the vena cava inferior. During the entire period of fœtal life, there remains an opening in the septum, which the valve of the foramen ovale, developed in the third month, imperfectly closes.

Bulbus Arteriosus.—The *bulbus arteriosus* which is originally a single tube, becomes gradually divided into two by the growth of an internal septum, which springs from the posterior wall, and extends forwards towards the front wall and downwards towards the ventricles. This partition takes a somewhat spiral direction, so that the two tubes (aorta and pulmonary artery) which result from its completion, do not run side by side, but are twisted round each other.

As the septum grows down towards the ventricles, it meets and coalesces with the upwardly growing ventricular septum, and thus from the right and left ventricles, which are now completely separate, arise respectively the pulmonary artery and aorta, which are also quite distinct. The auriculo-ventricular and semilunar valves are formed by the growth of folds of the endocardium.

At its first appearance the heart is placed just beneath the head of the fœtus, and is very large relatively to the whole body: but with the growth of the neck it becomes further and further removed from the head, and lodged in the cavity of the thorax.

Up to a certain period the auricular is larger than the ventricular division of the heart; but this relation is gradually reversed as development proceeds. Moreover, all through fœtal life, the walls of the right ventricle are of very much the same thickness as those of the left, which may probably be explained by the fact that in the fœtus the right ventricle has to propel the blood from the pulmonary artery into the aorta, and thence into the placenta, while in the adult it only drives the blood through the lungs.

Arteries.—The primitive aorta arises from the bulbus arteriosus and divides into two branches which arch backwards, one on each side of the foregut and unite again behind it, and in front of the notochord into a single vessel.

This gives off the two omphalo-mesenteric arteries, which distribute branches all over the yolk-sac ; this *area vasculosa* in the chick attaining a large development, and being limited all round by a vessel known as the sinus terminalis.

The blood is collected by the venous channels, and returned through the omphalo-mesenteric veins to the heart.

Behind this pair of primitive aortic arches, four more pairs make their appearance successively, so that there are five pairs in all, each one running along one of the visceral arches.

These five are never all to be seen at once in the embryo of higher animals, for the two anterior pairs gradually disappear, while the posterior ones are making their appearance, so that at length only three remain.

In Fishes, however, they all persist throughout life as the branchial arteries supplying the gills, while in Amphibia three pairs persist throughout life.

In Reptiles, Birds, and Mammals, further transformations occur.

In Reptiles the fourth pair remains throughout life as the permanent right and left aorta ; in Birds the right one remains as the permanent aorta, curving over the right bronchus instead of the left as in Mammals.

In Mammals the left fourth aortic arch developes into the permanent aorta, the right one remaining as the subclavian artery of that side. Thus the subclavian artery on the right side corresponds to the aortic arch on the left, and this homology is further confirmed by the fact that the recurrent laryngeal nerve hooks under the subclavian on the right side, and the aortic arch on the left.

The third aortic arch remains as the external carotid artery, while the fifth disappears on the right side, but on the left forms the pulmonary artery. The distal end of this arch originally opens into the descending aorta, and this communication (which is permanent throughout life in many reptiles on both sides of the body) remains throughout fœtal life under the name of *ductus arteriosus*: the branches of the pulmonary artery, to the right and left lung are very small, and most of the blood which is forced into the pulmonary artery passes through the wide ductus arteriosus into the descending aorta. All these points will become clear on reference to the accompanying diagram (fig. 439).

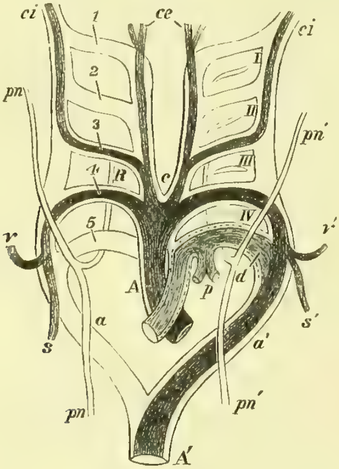


Fig. 439.—*Diagram of the aortic arches in a mammal*, showing transformations which give rise to the permanent arterial vessels. *A*, primitive arterial stem or aortic bulb, now divided into *A*, the ascending part of the aortic arch, and *p*, the pulmonary; *a a′*, right and left aortic roots; *A′*, descending aorta; 1, 2, 3, 4, 5, the five primitive aortic or branchial arches; *I, II, III, IV*, the four branchial clefts which, for the sake of clearness, have been omitted on the right side. The permanent systemic vessels are deeply, the pulmonary arteries, lightly shaded; the parts of the primitive arches which are transitory are simply outlined; *c*, placed between the permanent common carotid arteries; *c e*, external carotid arteries; *c i*, internal carotid arteries; *s*, right subclavian, rising from the right aortic root beyond the fifth arch; *v*, right vertebral from the same, opposite the fourth arch; *v′ s′*, left vertebral and subclavian arteries rising together from the left, or permanent aortic root, opposite the fourth arch; *p*, pulmonary arteries rising together from the left fifth arch; *d*, outer or back part of left fifth arch, forming ductus arteriosus; *p n*, *p n′*, right and left pneumogastric nerves, descending in front of aortic arches, with their recurrent branches represented diagrammatically as passing behind, to illustrate the relations of these nerves respectively to the right subclavian artery (4), and the arch of the aorta and ductus arteriosus (*d*). (Allen Thomson, after Rathke.)

As the umbilical vesicle dwindles in size, the portion of the omphalo-mesenteric arteries outside the body gradually disappears, the part inside the body remaining as the mesenteric arteries (figs. 440, 441).

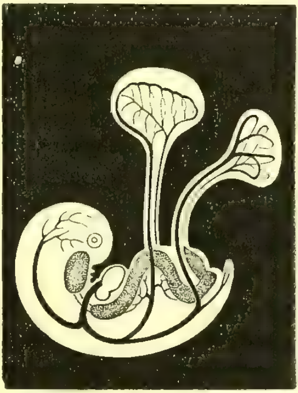


Fig. 440.—*Diagram of young embryo and its vessels*, showing course of circulation in the umbilical vesicle; and also that of the allantois (near the caudal extremity), which is just commencing. (Dalton.)

Meanwhile with the growth of the allantois two new arteries (umbilical) appear, and rapidly increase in size till they are the largest branches of the aorta: they are given off from the internal iliac arteries, and for a long time are considerably larger than the external iliacs which supply the comparatively small hind-limbs.

Veins.—The chief veins in the early embryo may be divided into two groups, visceral and parietal: the former includes the omphalo-mesenteric and umbilical, the latter the jugular and cardinal veins. The former may be first considered.

The earliest veins to appear in the fœtus are the omphalo-mesenteric which return the blood from the yolk-sac to the developing auricle. As soon as the placenta with its umbilical veins is developed, these unite with the omphalo-mesenteric, and thus the blood which reaches the auricle comes partly from the yolk-sac and partly from the placenta. The right omphalo-mesenteric and the right umbilical vein soon disappear, and the united left omphalo-mesenteric and umbilical veins pass through the developing liver on the way to the auricle. Two sets of vessels make their appearance in connection

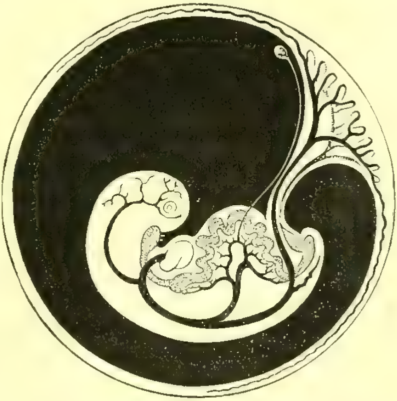


Fig. 441.—*Diagram of embryo and its vessels at a later stage*, showing the second circulation. The pharynx, œsophagus, and intestinal canal have become further developed, and the mesenteric arteries have enlarged, while the umbilical vesicle and its vascular branches are very much reduced in size. The large umbilical arteries are seen passing out in the placenta. (Dalton.)

with the liver (venæ hepaticæ advehentes, and revehentes), both opening into the united omphalo-mesenteric and umbilical veins, in such a way that a portion of the venous blood traversing the latter is diverted into the developing liver, and, having passed though its capillaries, returns to the umbilical vein through the venæ hepaticæ revehentes at a point nearer the heart (see fig. 442). The portion of vein between the afferent and efferent veins of the liver becomes the ductus venosus. The venæ hepaticæ advehentes become the right and left branches of the portal vein, the venæ hepaticæ revehentes become the hepatic veins, which open just at the junction of the ductus venosus with another large vein (vena cava inferior), which is now being developed. The mesenteric portion of the omphalo-mesenteric vein returning blood from the developing intestines remains as the mesenteric vein, which, by its union with the splenic vein forms the portal.

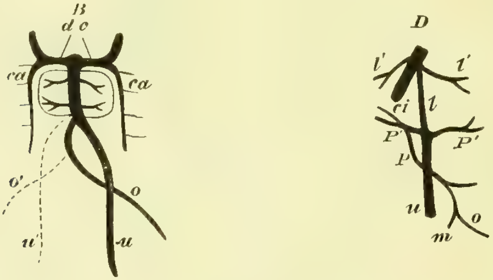


Fig. 442.—*Diagrams illustrating the development of veins about the liver.* *B*, *d c*, ducts of Cuvier, right and left; *c a*, right and left cardinal veins; *o*, left omphalo-mesenteric vein; *o'*, right omphalo-mesenteric vein, almost shrivelled up; *u*, *u'*, umbilical veins, of which *u'*, the right one, has almost disappeared. Between the venæ cardinales is seen the outline of the rudimentary liver, with its venæ hepaticæ advehentes, and revehentes; *D*, ductus venosus; *l'*, hepatic veins; *c i*, vena cava inferior; *P*, portal vein; *P' P'*, venæ advehentes; *m*, mesenteric veins. (Kölliker.)

Thus the fœtal liver is supplied with venous blood from two sources, through the umbilical and portal vein respectively. At birth the circulation through the umbilical vein of course completely ceases and the vessel begins at once to dwindle, so that now the only venous supply of the liver is through the portal vein. The earliest appearance of the *parietal* system of veins is the formation of two short transverse veins (ducts of Cuvier) opening into the auricle on either side, which result from the union of a jugular vein, collecting blood from the head and neck, and a cardinal vein which returns the blood from the Wolffian bodies, the vertebral column, and the parieties of the trunk. This arrangement persists throughout life in Fishes, but in Mammals the following transformations occur.

As the kidneys are developing a new vein appears (vena cava inferior), formed by the junction of their efferent veins. It receives branches from the legs (iliac) and increases rapidly in size as they grow: further up it receives the hepatic veins. The heart gradually descends into the thorax causing the ducts of Cuvier to become oblique instead of transverse. As the fore-limbs develop, the subclavian veins are formed.

A transverse communicating trunk now unites the two ducts of Cuvier, and gradually increases, while the left duct of Cuvier becomes almost entirely obliterated (all its blood passing by the communicating trunk to the right side) (fig. 443, C, D). The right duct of Cuvier remains as the right innominate vein, while the communicating branch forms the left innominate. The remnant of the left duct of Cuvier generally remains as a fibrous band, running obliquely down to the coronary vein, which is really the proximal part of the left duct of Cuvier. In front of the root of

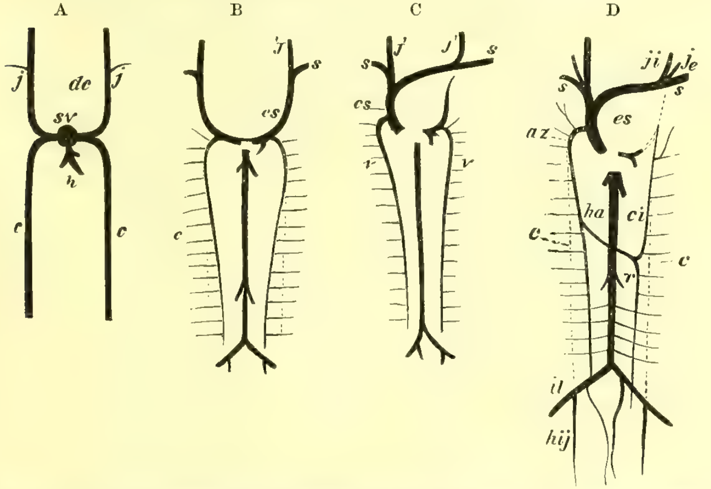


Fig. 443.—*Diagrams illustrating the development of the great veins.* *d c*, ducts of Cuvier; *j*, jugular veins; *h*, hepatic veins; *c*, cardinal veins; *s*, subclavian vein; *j i*, internal jugular vein; *j e*, external jugular vein; *a z*, azygos vein; *c i*, inferior vena cava; *r*, renal veins; *i l*, iliac veins; *h i j*, hypogastric veins. (Gegenbaur.)

the left lung, another relic may be found in the form of the so-called vestigial fold of Marshall, which is a fold of pericardium running in the same direction.

In many of the lower mammals, such as the rat, the left ductus Cuvieri remains as a left superior cava.

Meanwhile, a transverse branch carries across most of the blood of the left cardinal vein into the right; and by this union the great azygos vein is formed.

The upper portions of the left cardinal vein remain as the left superior intercostal and vena azygos minor (fig. 443, D).

Circulation of Blood in the Fœtus.

The circulation of blood in the fœtus differs considerably from that of the adult. It will be well, perhaps, to begin its description by tracing the course of the blood, which, after being carried out to the placenta by the two umbilical *arteries*, has returned, cleansed and replenished, to the fœtus by the umbilical vein.

It is at first conveyed to the under surface of the liver, and there the stream is divided,—a part of the blood passing straight on to the *inferior* vena cava, through a venous canal called the *ductus venosus*, while the remainder passes into the portal vein, and reaches the inferior vena cava only after circulating through the liver. Whether, however, by the direct route through the ductus venosus or by the roundabout way through the liver,—all the blood which is returned from the placenta by the umbilical vein reaches the inferior vena cava at last, and is carried by it to the right auricle of the heart, into which cavity is also pouring the blood that has circulated in the head and neck and arms, and has been brought to the auricle by the *superior* vena cava. It might be naturally expected that the two streams of blood would be mingled in the right auricle, but such is not the case, or only to a slight extent. The blood from the *superior* vena cava,—the less pure fluid of the two—passes almost exclusively into the *right* ventricle, through the auriculo-ventricular opening, just as it does in the adult; while the blood of the *inferior* vena cava is directed by a fold of the lining membrane of the heart, called the *Eustachian valve*, through the foramen ovale into the *left* auricle, whence it passes into the *left* ventricle, and out of this into the aorta, and thence to all the body. The blood of the *superior* vena cava, which, as before said, passes into the right ventricle, is sent out thence in small amount through the pulmonary artery to the lungs, and thence to the *left* auricle, as in the adult. The greater part, however, by far, does not go to the lungs, but instead, passes through a canal, the *ductus arteriosus*, leading from the pulmonary artery into the aorta just below the origin of the three great

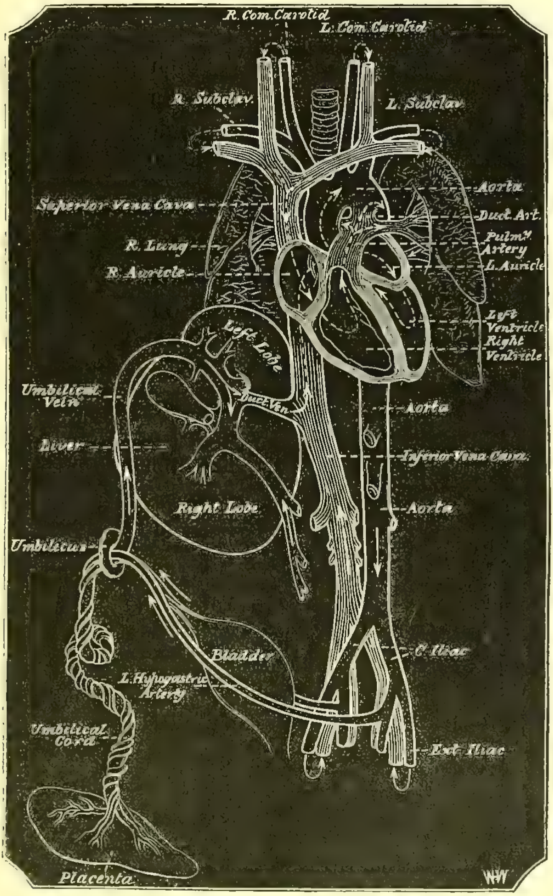


Fig. 444.—*Diagram of the Fœtal Circulation.*

vessels which supply the upper parts of the body; and there meeting that part of the blood of the inferior vena cava which has not gone into these large vessels, it is distributed with it to the trunk and lower parts,—a portion passing out by way of the two umbilical *arteries* to the placenta. From the placenta it is returned by the umbilical *vein* to the under surface of the liver, from which the description started.

Changes after Birth.—After birth the foramen ovale closes, and so do the ductus arteriosus and ductus venosus, as well as the umbilical vessels; so that the two streams of blood which arrive at the right auricle by the superior and inferior vena cava respectively, thenceforth mingle in this cavity of the heart, and passing into the right ventricle, go by way of the pulmonary artery to the lungs, and through these, after purification, to the left auricle and ventricle, to be distributed over the body. (See Chapter on Circulation.)

Development of the Nervous System.

Nerves.—All the spinal nerves are derived from the mesoblast; also all the cranial nerves, except the optic and olfactory, which are outgrowths of the anterior cerebral vesicles. From the same middle layer of the embryo are also derived the ganglia connected with these nerves, and the whole sympathetic system of nerves and ganglia.

Spinal Cord.—Both the brain and spinal cord have a different origin from that of the nerves which arise from them. These nerve-centres are developed entirely from the epiblast (possibly, however, a portion of the spinal cord originates in the mesoblast); while the nerves, as we have seen, are formed from mesoblast. The spinal cord is developed out of the primitive medullary tube which results from the folding in of the dorsal laminæ (*m*, fig. 411).

Soon after it has closed in, this tube is found to be somewhat oval in section, with a central canal, which, in sections, presents the appearance of an elongated slit, slightly expanded at each end. The two opposite sides unite (fig. 445) in the centre of the slit dividing it into an anterior portion (the permanent central canal of the cord) and a posterior, which makes its way to the free surface, and persists as the posterior fissure of the cord, lodging a very fine process of pia mater.

At this period the cord consists almost entirely of grey matter, but the white matter, which is derived probably from the surrounding mesoblast, becomes deposited around it on all sides, growing up especially on the anterior surface of the cord into the two anterior columns. These are separated by a fissure (anterior fissure of cord), which of course deepens as the columns bounding it become more prominent (fig. 445).

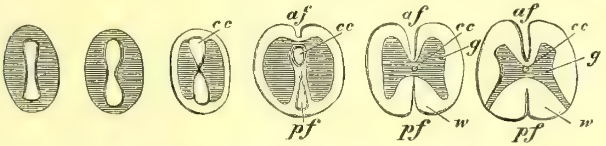


Fig. 445.—*Diagram of development of spinal cord: cc*, central canal; *af*, anterior fissure; *pf*, posterior fissure; *g*, grey matter; *w*, white matter. *For further explanation see text.*

By the development of various commissures, the cord is completed.

When it first appears, the spinal cord occupies the whole length of the medullary canal, but as development proceeds, the spinal column grows more rapidly than the contained cord, so that the latter appears as if drawn up till, at birth, it is opposite the third lumbar vertebra, and in the adult opposite the first lumbar. In the same way the increasing obliquity of the spinal nerves in the neural canal, as we approach the lumbar region, and the "cauda equina" at the lower end of the cord, are accounted for.

Brain.—We have seen (p. 763) that the front portion of the medullary canal is almost from the first widened out and divided into three vesicles. From the anterior vesicle (thalamencephalon) the two primary optic vesicles are budded off laterally: their further history will be traced in the next section. Somewhat later, from the same vesicle the rudiments of the hemispheres appear in the form of two outgrowths at a higher level, which grow upwards and backwards. These form the *prosencephalon.*

In the walls of the posterior (third) cerebral vesicle, a thickening appears (rudimentary cerebellum) which becomes separated from the rest of the vesicle by a deep inflection.

At this time there are two chief curvatures of the brain (fig. 446, 3). (1.) A sharp bend of the whole cerebral mass downwards round the end of the notochord, by which the anterior vesicle, which was the highest of the three, is bent downwards, and the middle one comes to occupy the highest position. (2.) A sharp bend, with the convexity forwards, which runs in from behind beneath the rudimentary cerebellum separating it from the medulla.

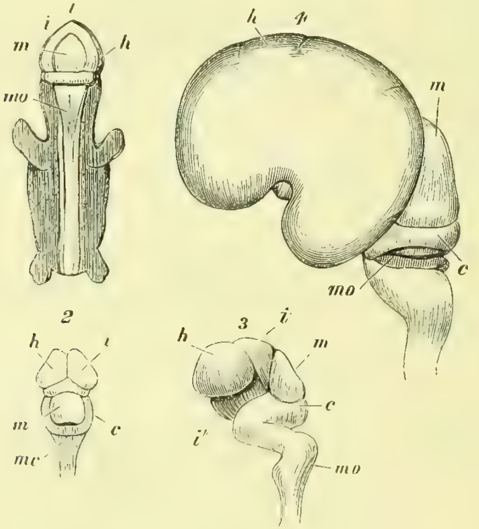


Fig. 446.—*Early stages in development of human brain* (magnified). 1, 2, 3, are from an embryo about seven weeks old; 4, about three months old. *m*, middle cerebral vesicle (mesencephalon); *c*, cerebellum; *m o*, medulla oblongata; *i*, thalamencephalon; *h*, hemispheres; *i′*, infundibulum; Fig. 3 shows the several curves which occur in the course of development; Fig. 4 is a lateral view, showing the great enlargement of the cerebral hemispheres which have covered in the thalami, leaving the optic lobes, *m*, uncovered. (Kölliker.)

N.B.—In fig. 2 the line *i* terminates in the right hemisphere, it ought to be continued into the thalamencephalon.

Thus, five fundamental parts of the fœtal brain may be distinguished, which, together with the parts developed from them may be presented in the following tabular view.

Table of Parts Developed from Fundamental Parts of Brain.

I. Anterior Primary Vesicle.	1. Prosencephalon.	Cerebral hemispheres, corpora striata, corpus callosum, fornix, lateral ventricles, olfactory bulb (Rhinencephalon).
	2. Thalamencephalon (Diencephalon).	Thalami optici, pineal gland, pituitary body, third ventricle, optic nerve (primarily).
II. Middle Primary Vesicle.	3. Mesencephalon.	Corpora quadrigemina, crura cerebri, aqueduct of Sylvius, optic nerve (secondarily).
III. Posterior Primary Vesicle.	4. Epencephalon.	Cerebellum, pons Varolii, anterior part of fourth ventricle.
	5. Metencephalon.	Medulla oblongata, fourth ventricle, auditory nerve.

(*Quain's Anatomy.*)

The cerebral hemispheres grow rapidly upwards and backwards, while from their inferior surface the olfactory bulbs are budded off, and the thalamencephalon, from which they spring, remains to form the third ventricle and optic thalami. The middle cerebral vesicle (mesencephalon) for some time is the most prominent part of the fœtal brain, and in Fishes, Amphibia, and Reptiles, it remains uncovered through life as the optic lobes. But in Birds the growth of the cerebral hemispheres thrusts the optic lobes down laterally, and in Mammalia completely overlaps them.[1]

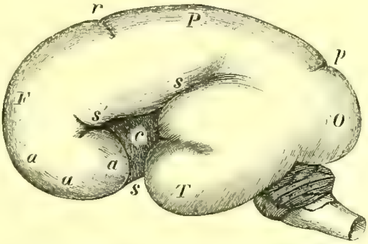


Fig. 447.—*Side view of fœtal brain at six months*, showing commencement of formation of the principal fissures and convolutions. *F*, frontal lobe; *P*, parietal; *O*, occipital; *T*, temporal; *a a a*, commencing frontal convolutions; *s*, Sylvian fissure; *s'*, its anterior division; *c*, within it the central lobe or island of Reil; *r*, fissure of Rolando; *p*, perpendicular fissure. (R. Wagner.)

In the lower Mammalia the backward growth of the hemispheres ceases as it were, but in the higher groups, such as the monkeys and man, they grow still further back, until they completely cover in the cerebellum, so that on looking down on the brain from above, the cerebellum is quite concealed from view. The surface of the hemispheres is at first quite smooth, but as early as the third month the great Sylvian fissure begins to be formed (fig. 446, 4).

The next to appear is the parieto-occipital or perpendicular fissure; these two great fissures, unlike the rest of the sulci, are formed by a curving round of the whole cerebral mass.

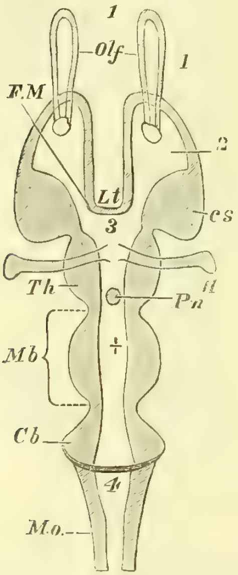


Fig. 448.—*Diagrammatic horizontal section of a Vertebrate brain.* The figures serve both for this and the next diagram. *Mb*, mid brain: what lies in front of this is the fore-, and, what lies behind, the hind-brain; *Lt*, lamina terminalis; *Olf*, olfactory lobes; *Hmp*, hemispheres; *Th.E*, thalamencephalon; *Pn*, pineal gland; *Py*, pituitary body; *FM*, foramen of Munro; *cs*, corpus striatum; *Th*, optic thalamus; *CC*, crura cerebri: the mass lying above the canal represents the corpora quadrigemina; *Cb*, cerebellum; *I—IX.*, the nine pairs of cranial nerves; 1, olfactory ventricle; 2, lateral ventricle; 3, third ventricle; 4, fourth ventricle; +, iter a tertio ad quartum ventriculum. (Huxley.)

In the sixth month the fissure of Rolando appears: from this time till the end of fœtal life the brain grows rapidly in size, and the convolutions appear in quick succession; first the great primary ones are sketched out, then the secondary, and lastly the tertiary ones in the sides of the fissures. The commissures of the brain (anterior, middle, and posterior), and the corpus callosum, are developed by the growth of fibres across the middle line.

The Hippocampus major is formed by the folding in of the grey matter from the exterior into the latter ventricles. The essential points in the structure and arrangement of the various parts of the brain, are diagrammatically shown in the two accompanying figures (figs. 448, 449).

Development of the Organs of Sense.

Eye.—Soon after the first three cerebral vesicles have become distinct from each other, the anterior one sends out a lateral vesicle from each side, (primary optic vesicle), which grows out towards the free surface, its cavity of course communicating with that of the cerebral vesicle through the canal in its pedicle. It is soon met and invaginated by an in-growing process from the epiblast (fig. 450), very much as the growing tooth is met by the process of epithelium which produces the enamel organ. This process of the epiblast is at first a depression which ultimately becomes closed in at the edges so as to produce a hollow ball, which is thus completely severed from the epithelium with which it was originally continuous. From this hollow ball the crystalline lens is developed. By the ingrowth of the lens the anterior wall of the primary optic vesicle is forced back nearly into contact with the posterior, and thus the primary optic vesicle is almost obliterated. The cells in the anterior wall are much longer than those of the posterior wall; from the former the retina proper is developed, from the latter the retinal pigment.

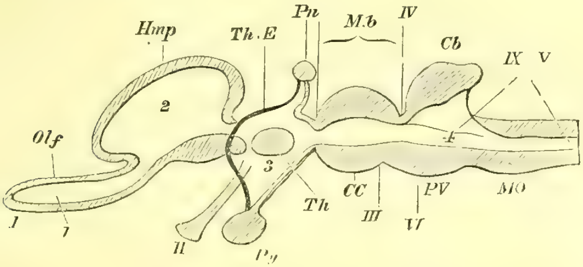


Fig. 449.—Longitudinal and vertical diagrammatic section of a *Vertebrate brain.* Letters as before. Lamina terminalis is represented by the strong black line joining *Pn* and *Py.* (Huxley.)

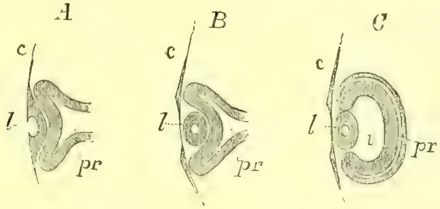


Fig. 450.—*Longitudinal section of the primary optic vesicle* in the chick magnified (from Remak).—A, from an embryo of sixty-five hours; B, a few hours later; C, of the fourth day; *c*, the corneous layer or epidermis, presenting in A, the open depression for the lens, which is closed in B and C; *l*, the lens follicle and lens; *pr*, the primary optic vesicle; in A and B, the pedicle is shown; in C, the section being to the side of the pedicle, the latter is not shown; *v*, the secondary ocular vesicle and vitreous humour.

The cup-shaped hollow in which the lens is now lodged is termed the secondary optic vesicle: its walls grow up all round, leaving, however, a slit at the lower part.

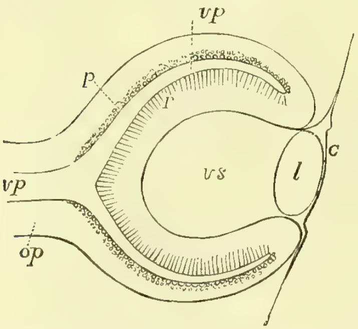


Fig. 451.—*Diagrammatic sketch of a vertical longitudinal section through the eyeball of a human fœtus of four weeks.* The section is a little to the side, so as to avoid passing through the ocular cleft; *c*, the cuticle where it becomes later the corneal epithelium; *l*, the lens; *op*, optic nerve formed by the pedicle of the primary optic vesicle; *vp*, primary medullary cavity or optic vesicle; *p*, the pigment layer of the retina; *r*, the inner wall forming the retina proper; *vs*, secondary optic vesicle containing the rudiment of the vitreous humour. × 100. (Kölliker.)

Choroidal Fissure.—Through this slit (fig. 452), often termed the *choroidal fissure*, a process of mesoblast containing numerous blood-vessels projects, and occupies the cavity of the secondary optic vesicle behind the lens, filling it with vitreous humour and furnishing the lens capsule and the capsulo-pupillary membrane. This process in Mammals projects, not only into the secondary optic vesicle, but also into the pedicle of the primary optic vesicle invaginating it for some distance from beneath, and thus carrying up the *arteria centralis retinæ* into its permanent position in the centre of the optic nerve.

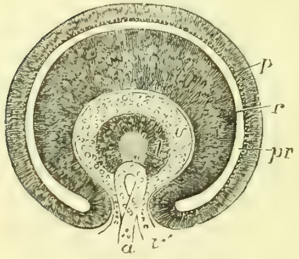


Fig. 452.—*Transverse vertical section of the eyeball of a human embryo of four weeks.* The anterior half of the section is represented: *pr*, the remains of the cavity of the primary optic vesicle; *p*, the inner part of the outer layer forming the retinal pigment; *r*, the thickened inner part giving rise to the columnar and other structures of the retina; *v*, the commencing vitreous humour within the secondary optic vesicle; *v'*, the ocular cleft through which the loop of the central blood-vessel, *a*, projects from below; *l*, the lens with a central cavity. × 100. (Kölliker.)

This invagination of the optic nerve does not occur in *birds*, and consequently no arteria centralis retinæ exists in them. But they possess an important permanent relic of the original protrusion of the mesoblast through the choroidal fissure, forming the *pecten*, while a remnant of the same fissure sometimes occurs in man under the name coloboma iridis. The cavity of the primary optic vesicle becomes completely obliterated, and the rods and cones come into apposition with the pigment layer of the retina.

The cavity of its pedicle disappears and the solid optic nerve is formed. Meanwhile the cavity which existed in the centre of the primitive lens becomes filled up by the growth of fibres from its posterior wall. The epithelium of the cornea is developed from the epiblast, while the corneal tissue proper is derived from the mesoblast which intervenes between the epiblast and the primitive lens which was originally continuous with it. The sclerotic coat is developed round the eye-ball from the general mesoblast in which it is imbedded.

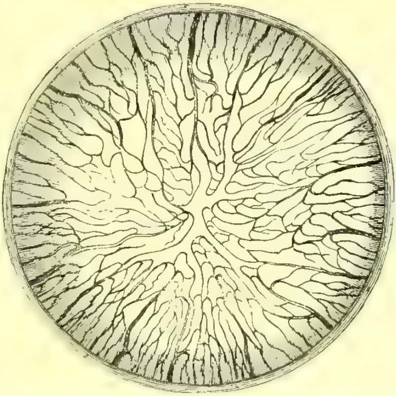


Fig. 453.—*Blood-vessels of the capsulo-pupillary membrane of a new-born kitten*, magnified. The drawing is taken from a preparation injected by Tiersch, and shows in the central part the convergence of the net-work of vessels in the pupillary membrane. (Kolliker.)

The iris is formed rather late, as a circular septum projecting inwards, from the fore part of the choroid, between the lens and the cornea. In the eye of the fœtus of Mammalia, the pupil is closed by a delicate membrane, the *membrana pupillaris*, which forms the front portion of a highly vascular membrane that, in the fœtus, surrounds the lens, and is named the *membrana capsulo-pupillaris* (fig. 453). It is supplied with blood by a branch of the *arteria centralis retinæ*, which, passing forwards to the back of the lens, there subdivides. The membrana capsulo-pupillaris withers and disappears in the human subject a short time before birth.

The eyelids of the human subject and mammiferous animals like those of birds, are first developed in the form of a ring. They then extend over the globe of the eye until they meet and become firmly agglutinated to each other. But before birth, or in the Carnivora after birth, they again separate.

Ear.—Very early in the development of the embryo a depression or ingrowth of the epiblast occurs on each side of the head which deepens and soon becomes a closed follicle. This *primary otic vesicle* which closely corresponds in its formation to the lens follicle in the eye, sinks down to some distance from the free surface; from it are developed the epithelial lining of the *membranous* labyrinth of the internal ear, consisting of the vestibule and its semicircular canals and the scala media of the cochlea. The surrounding mesoblast gives rise to the various fibrous bony and cartilaginous parts which complete and enclose this membranous labyrinth, the bony semicircular canals, the walls of the cochlea with its scala vestibuli and scala tympani. In the mesoblast, between the primary otic vesicle and the brain, the auditory nerve is gradually differentiated and forms its central and peripheral attachments to the brain and internal ear respectively. According to some authorities, however, it is said to take its origin from and grow out of the hind brain.

The Eustachian tube, the cavity of the tympanum, and the external auditory passage, are remains of the first branchial cleft. The membrana tympani divides the cavity of this cleft into an internal space, the tympanum, and the external meatus. The mucous membrane of the mouth, which is prolonged in the form of a diverticulum through the Eustachian tube into the tympanum, and the external cutaneous system, come into relation with each other at this point; the two membranes being separated only by the proper membrane of the tympanum.

The pinna or external ear is developed from a process of integument in the neighbourhood of the first and second visceral arches, and probably corresponds to the gill-cover (operculum) in fishes.

Nose.—The nose originates like the eye and ear in a depression of the superficial epiblast at each side of the fronto-nasal process (primary olfactory groove), which is at first completely separated from the cavity of the mouth, and gradually extends backwards and downwards till it opens into the mouth.

The outer angles of the fronto-nasal process, uniting with the maxillary process on each side, convert what was at first a groove into a closed canal.

Development of the Alimentary Canal.

The alimentary canal in the earliest stages of its development consists of three distinct parts—the fore and hind gut ending blindly at each end of the body, and a middle segment which communicates freely on its ventral surface with the cavity of the yelk-sac through the vitelline or omphalo-mesenteric duct (p. 767)

From the fore-gut are formed the pharynx, œsophagus, and stomach; from the hind-gut, the lower end of the colon and the rectum. The mouth is developed by an involution of the epiblast between the maxillary and mandibular processes, which becomes deeper and deeper till it reaches the blind end of the fore-gut, and at length communicates freely with the pharynx by the absorption of the partition between the two.

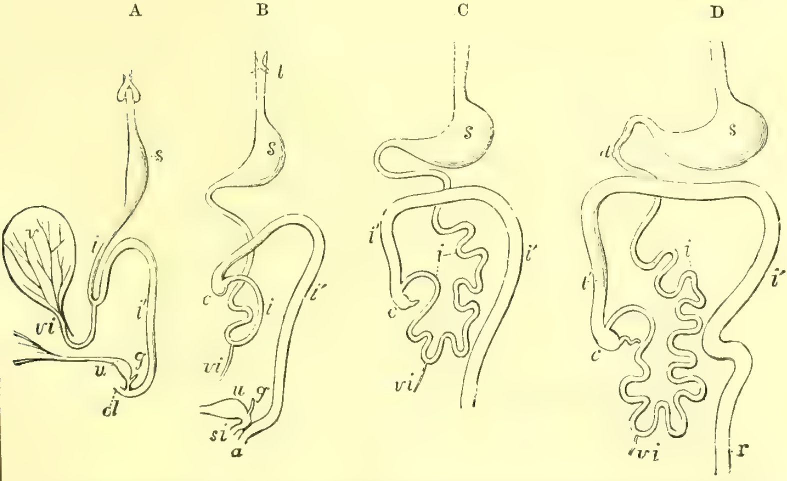


Fig. 454.—*Outlines of the form and position of the alimentary canal in successive stages of its development.* A, alimentary canal, &c., in an embryo of four weeks; B, at six weeks; C, at eight weeks; D, at ten weeks; *l*, the primitive lungs connected with the pharynx; *s*, the stomach; *d*, the duodenum; *i*, the small intestine; *i'*, the large; *c*, the cæcum and vermiform appendage; *r*, the rectum; *cl*, in A, the cloaca; *a*, in B, the anus distinct from *s i*, the sinus uro-genitalis; *v*, the yelk-sac; *v i*, the vitello-intestinal duct; *u*, the urinary bladder and urachus leading to the allantois; *g*, genital ducts. (Allen Thomson.)

At the other end of the alimentary canal the anus is formed in a precisely similar way by an involution from the free surface, which at length opens into the hind-gut. When the depression from the free surface does not reach the intestine, the condition known as imperforate anus results. A similar condition may exist at the other end of the alimentary canal from the failure of the involution which forms the mouth, to meet the fore-gut. The middle portion of the digestive canal becomes more and more closed in till its originally wide communication with the yelk-sac becomes narrowed down to a small duct (vitelline). This duct usually completely disappears in the adult, but occasionally the proximal portion remains as a diverticulum from the intestine. Sometimes a fibrous cord attaching some part of the intestine to the umbilicus, remains to represent the vitelline duct. Such a cord has been known to cause in after-life strangulation of the bowel and death.

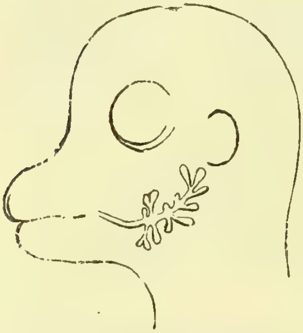


Fig. 455.—*First appearance of the parotid gland in the embryo of a sheep.*

The alimentary canal lies in the form of a straight tube close beneath the vertebral column, but it gradually becomes divided into its special parts, stomach, small intestine, and large intestine (fig. 454), and at the same time comes to be suspended in the abdominal cavity by means of a lengthening mesentery formed from the splanchnopleure which attaches it to the vertebral column. The stomach originally has the same direction as the rest of the canal; its cardiac extremity being superior, its pylorus inferior. The changes of position which the alimentary canal undergoes may be readily gathered from the accompanying figures (fig. 454).

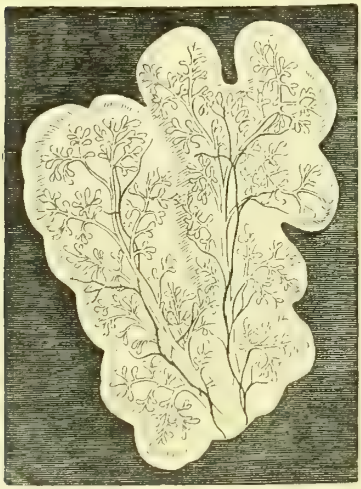


Fig. 456.—*Lobules of the parotid*, with the salivary ducts, in the embryo of the sheep, at a more advanced stage.

Pancreas and Salivary Glands.—The principal glands in connection with the intestinal canal are the salivary, pancreas, and the liver. In Mammalia, each salivary gland first appears as a simple canal with bud-like processes (fig. 455), lying in a gelatinous nidus or blastema, and communicating with the cavity of the mouth. As the development of the gland advances, the canal becomes more and more ramified, increasing at the expense of the blastema in which it is still enclosed. The branches or salivary ducts constitute an independent system of closed tubes (fig. 456). The pancreas is developed exactly as the salivary glands, but is developed from the hypoblast lining the intestine, while the salivary glands are formed from the epiblast lining the mouth.

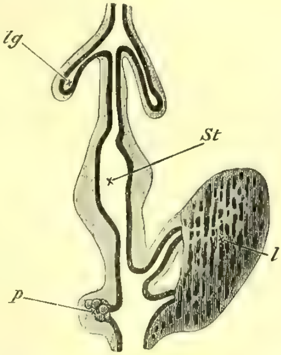


Fig. 457.—*Diagram of part of digestive tract of a chick* (4th day). The black line represents hypoblast, the outer shading mesoblast: *l g*, lung diverticulum, with expanded end forming primary lung-vesicle; *S t*, stomach; *l*, two hepatic diverticula, with their terminations united by solid rows of hypoblast cells; *p*, diverticulum of the pancreas with the vesicular diverticula coming from it. (Gotte.)

Liver.—The liver is developed by the protrusion, as it were, of a part of the walls of the intestinal canal, in the form of two conical hollow branches which embrace the common venous stem (figs. 457, 458). The outer part of these cones involves the omphalo-mesenteric vein, which breaks up in its interior into a plexus of capillaries, ending in venous trunks for the conveyance of the blood to the heart. The inner portion of the cones consists of a number of solid cylindrical masses of cells, derived probably from the hypoblast, which become gradually

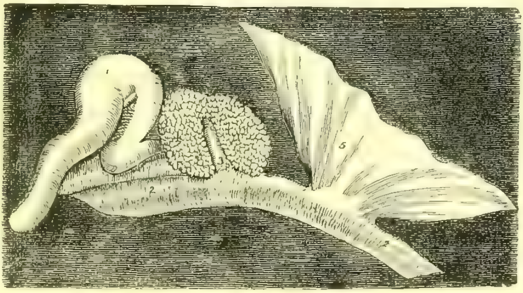


Fig. 458.—*Rudiments of the liver on the intestine of a chick* at the fifth day of incubation. 1, heart; 2, intestine; 3, diverticulum of the intestine in which the liver (4) is developed; 5, part of the mucous layer of the germinal membrane. (Müller.)

hollowed by the formation of the hepatic ducts, and among which blood-vessels are rapidly developed. The gland-cells of the organs are derived from the hypoblast, the connective tissue and vessels without doubt from the mesoblast. The gall-bladder is developed as a diverticulum from the hepatic duct. The spleen, lymphatic, and thymus glands are developed from the mesoblast: the thyroid partly also from the hypoblast which grows into it as a diverticulum from the fore-gut.

Development of the Respiratory Apparatus.

The lungs, at their first development, appear as small tubercles, or diverticular from the abdominal surface of the œsophagus. The two diverticula at first open directly into the œsophagus, but as they grow, a separate tube (the future trachea) is formed at their point of fusion, opening into the œsophagus on its anterior surface. These primary diverticula of the hypoblast of the alimentary canal send off secondary branches into the surrounding mesoblast, and these again give off tertiary branches, forming the air-cells. Thus we have the lungs formed: the epithelium lining their air cells, bronchi, and trachea being derived from the hypoblast, and all the rest of the lung-tissue, nerves, lymphatics, and blood-vessels, cartilaginous rings, and muscular fibres of the bronchi from the mesoblast. The diaphragm is early developed.

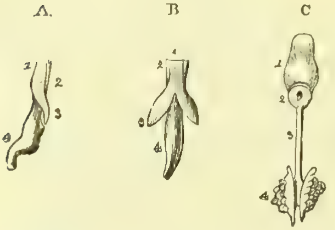


Fig. 459 *illustrates the development of the respiratory organs.* A, is the œsophagus of a chick on the fourth day of incubation, with the rudiments of the trachea on the lung of the left side, viewed laterally; 1, the inferior wall of the œsophagus; 2, the upper wall of the same tube; 3, the rudimentary lung; 4, the stomach. B, is the same object seen from below, so that both lungs are visible. C, shows the tongue and respiratory organs of the embryo of a horse: 1, the tongue; 2, the larynx; 3, the trachea; 4, the lungs, viewed from the upper side. (After Rathke.)

The Wolffian Bodies, Urinary Apparatus, and Sexual Organs.

The Wolffian bodies are organs peculiar to the embryonic state, and may be regarded as *temporary*, rather than *rudimental*, kidneys; for although they seem to discharge the functions of these latter organs, they are not developed into them.

Appearance of first rudiments.—The Wolffian duct makes its appearance at an early stage in the history of the embryo, as a cord running longitudinally on each side in the mass of mesoblast, which lies just external to the protovertebræ (*ung*, fig. 460). This cord, at first solid, becomes gradually hollowed out to form a tube (Wolffian duct) which sinks down till it projects beneath the lining membrane into the pleuro-peritoneal cavity.

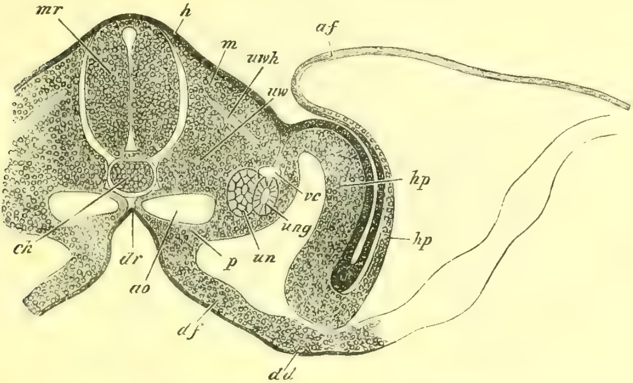


Fig. 460.—*Transverse of embryo chick* (third day). *m r*, rudimentary spinal cord; the primitive central canal has become constricted in the middle; *c h*, notochord; *u w h*, primordial vertebral mass; *m*, muscle-plate; *d r*, *d f*, hypoblast and visceral layer of mesoblast lining groove, which is not yet closed in to form the intestines; *a o*, one of the primitive aortæ; *u n*, Wolffian body; *u n g*, Wolffian duct; *v c*, vena cardinalis; *h*, epiblast; *h p*, somatopleure and its reflection to form *a f*, amniotic fold; *p*, pleuroperitoneal cavity. (Kölliker.)

The primitive tube thus formed sends off secondary diverticula at frequent intervals which grow into the surrounding mesoblast: tufts of vessels grow into the blind ends of these tubes, invaginating them and producing "Malpighian bodies" very similar in appearance to those of the permanent kidney, which constitute the substance of the Wolffian body. Meanwhile another portion of mesoblast between the Wolffian body and the mesentery projects in the form of a ridge, covered on its free surface with epithelium termed "germ epithelium." From this projection is developed the reproductive gland (ovary or testis as the case may be).

Simultaneously, on the outer wall of the Wolffian body, between it and the body-wall on each side, an involution is formed from the pleuro-peritoneal cavity in the form of a longitudinal furrow, whose edges soon close over to form a duct (Müller's duct).

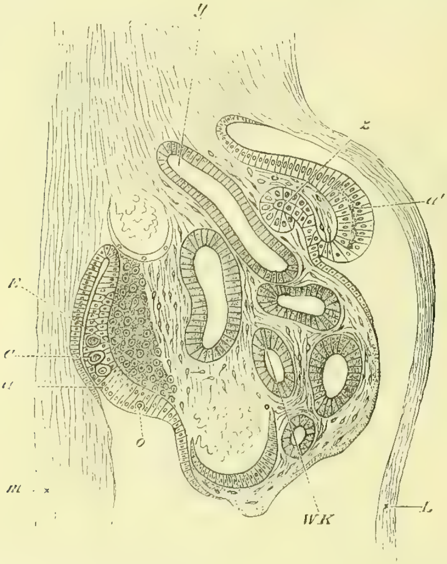


Fig. 461.—*Section of intermediate cell-mass on the fourth day.* *m*, mesentery; *L*, somatopleure; *a'*, germinal epithelium, from which *z*, the duct of Müller, becomes involuted; *a*, thickened part of germinal epithelium in which the primitive ova *C* and *o*, are lying; *E*, modified mesoblast, which will form the stroma of the ovary; *W K*, Wolffian body; *y*, Wolffian duct; × 160. (Waldeyer.)

All the above points are shown in the accompanying figures, 460, 461, 462, 463.

The Wolffian bodies, or *temporary* kidneys, as they may be termed, give place at an early period in the human fœtus to their successors, the *permanent* kidneys, which are developed behind them. They diminish rapidly in size, and by the end of the third month have almost entirely disappeared. In connection, however, with their upper part, in the male, there are developed from a new mass of blastema, the *vasa efferentia*, *coni vasculosi*, and *globus major* of the epididymis; and thus is brought about a direct connection between the secreting part of the testicle and its duct (Cleland, Banks). The Wolffian *ducts* persist in the male, and are developed to form the body and globus minor of the epididymis, the vas

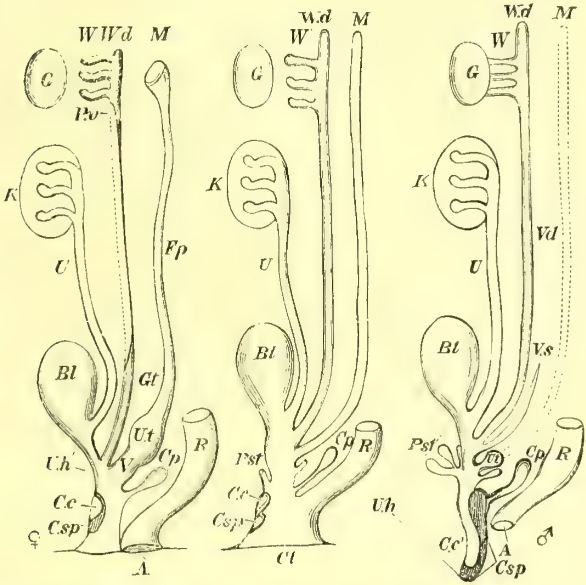


Fig. 462.—*Diagram showing the relations of the female (the left-hand figure ♀) and of the male (the right hand figure ♂) reproductive organs to the general plan (the middle figure) of these organs in the higher vertebrata* (including man). *C l*, cloaca; *R*, rectum; *B l*, urinary bladder; *U*, ureter; *K*, kidney; *U h*, urethra; *G*, genital gland, ovary or testis; *W*, Wolffian body; *W d*, Wolffian duct; *M*, Müllerian duct; *P s t*, prostate gland; *C p*, Cowper's gland; *C s p*, corpus spongiosum; *C c*, corpus cavernosum.

In the female.—*V*, vagina; *U t*, uterus; *F p*, Fallopian tube; *G t*, Gaertner's duct; *P r*, parovarium; *A*, anus; *C c*, *C s p*, clitoris.
In the male.—*C s p*, *C c*, penis; *U t*, uterus masculinus; *V s*, vesicula seminalis; *V d*, vas deferens. (Huxley.)

deferens, and ejaculatory duct on each side, the vesiculæ seminales forming diverticula from their lower part. In the female a small relic of the Wolffian body persists as the "parovarium;" in the male a similar relic is termed the "organ of Giraldès." The lower end of the Wolffian duct remains in the female as the "duct of Gaertner" which descends towards, and is lost upon, the anterior wall of the vagina.

From the lower end of the Wolffian duct a diverticulum grows back along the body of the embryo towards its anterior extremity, and ultimately forms the ureter. Secondary diverticula are given off from it and grow into the surrounding blastema of blood-vessels and cells.

Malpighian bodies are formed just as in the Wolffian body, by the invagination of the blind knobbed end of these diverticula by a tuft of vessels (fig. 463). This process is precisely similar to the invagination of the primary optic vesicle by the rudimentary lens. Thus the kidney is developed, consisting at first of a number of separate *lobules;* this condition remaining throughout life in many of the lower animals, *e.g.*, seals and whales, and traces of this lobulation being visible in the human fœtus at birth. In the adult all the lobules are fused into a compact solid organ.

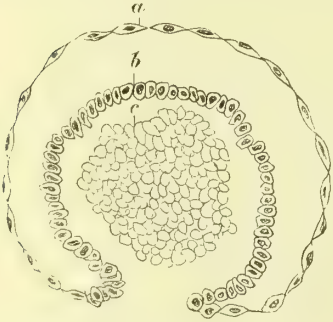


Fig. 463.—*Transverse section of a developing Malpighian capsule and tuft* (human). From a fœtus at about the fourth month; *a*, flattened cells growing to form the capsule; *b*, more rounded cells, continuous with the above, reflected round *c*, and finally enveloping it; *c*, mass of embryonic cells which will later become developed into blood-vessels. × 300. (W. Pye.)

The supra-renal capsules originate in a mass of mesoblast just above the kidneys; soon after their first appearance they are very much larger than the kidneys (see fig. 464), but by the more rapid growth of the latter this relation is soon reversed.

Later Development.

The first appearance of the generative gland has been already described: for some time it is impossible to determine whether an ovary or testis will be developed from it; gradually however the special characters belonging to one of them appear, and in either case the organ soon begins to assume a relatively lower position in the body; the ovaries being ultimately placed in the pelvis; while towards the end of fœtal existence the testicles descend into the scrotum, the testicle entering the internal inguinal ring in the seventh month of fœtal life, and completing its descent through the inguinal canal and external ring into the scrotum by the end of the eighth month. A pouch of peritoneum, the *processus vaginalis*, precedes it in its descent, and ultimately forms the tunica vaginalis or serous covering of the organ; the communication between the tunica vaginalis and the cavity of the peritoneum being closed only a short time before birth. In its descent, the testicle or ovary of course retains the blood-vessels, nerves, and lymphatics, which were supplied to it while in the lumbar region, and which are compelled to follow it, so to speak, as it assumes a lower position in the body. Hence the explanation of the otherwise strange fact of the origin of these parts at so considerable a distance from the organ to which they are distributed.

Descent of the Testicles into Scrotum.—The means by which the descent of the testicles into the scrotum is effected are not fully and exactly known. It was formerly believed that a membranous and partly muscular cord, called the *gubernaculum testis*, which extends while the testicle is yet high in the abdomen, from its lower part, through the abdominal wall (in the situation of the inguinal canal) to the front of the pubes and lower part of the scrotum, was the agent by the contraction of which the descent was effected. It is now generally believed, however, that such is not the case; and that the descent of the testicle and ovary is rather the result of a general process of development in these and neighbouring parts, the tendency of which is to produce this change in the relative position of these organs. In other words, the descent is not the result of a mere mechanical action, by which the organ is dragged down to a lower position, but rather one change out of many which attend the gradual development and re-arrangement of these organs. It may be repeated, however, that the details of the process by which the descent of the testicle into the scrotum is effected are not accurately known.

The homologue, in the female, of the gubernaculum testis, is a structure called the *round ligament of the uterus*, which extends through the inguinal canal, from the outer and upper part of the uterus to the subcutaneous tissue in front of the symphysis pubis.

At a very early stage of fœtal life, the Wolffian ducts, ureters, and Müllerian ducts, open into a receptacle formed by the lower end of the allantois, or rudimentary bladder; and as this communicates with the lower extremity of the intestine, there is for the time, a common receptacle or *cloaca* for all these parts, which opens to the exterior of the body through a part corresponding with the future anus, an arrangement which is permanent in Reptiles, Birds, and some of the lower Mammalia. In the human fœtus, however, the intestinal portion of the cloaca is cut off from that which belongs to the urinary and generative organs; a separate passage or canal to the exterior of the body, belonging to these parts, being called the *sinus urogenitalis.* Subsequently, this canal is divided, by a process of division extending from before backwards or from above downwards, into a 'pars urinaria' and a 'pars genitalis.' The former, continuous with the *urachus,* is converted into the urinary bladder.

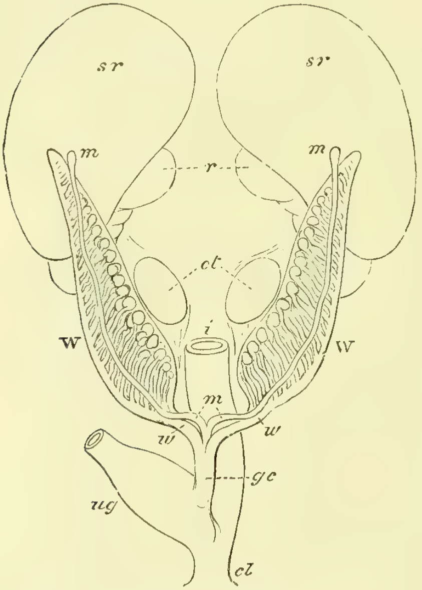


Fig. 464.—*Diagram of the Wolffian bodies, Müllerian ducts and adjacent parts previous to sexual distinction,* as seen from before. *sr,* the supra-renal bodies; *r,* the kidneys; *ot,* common blastema of ovaries or testicles; W, Wolffian bodies; *w,* Wolffian ducts; *m, m,* Müllerian ducts; *g c,* genital cord; *ug,* sinus urogenitalis; *i,* intestine; *cl,* cloaca. (Allen Thompson.)

The Fallopian tubes, the uterus, and the vagina are developed from the Müllerian ducts (fig. 464, *m* and fig. 465) whose first appearance has been already described. The two Müllerian ducts are united below into a single cord, called the *genital cord,* and, from this are developed the vagina, as well as the cervix and the lower portion of the body of the uterus; while the ununited portion of the duct on each side forms the upper part of the uterus, and the Fallopian tube. In certain cases of arrested or abnormal development, these portions of the Müllerian ducts may not become fused together at their lower extremities, and there is left a cleft or horned condition of the upper part of the uterus resembling a condition which is permanent in certain of the lower animals.

In the male, the Müllerian ducts have no special function, and are but slightly developed. The hydatid of Morgagni is the remnant of the upper part of the Müllerian duct. The small prostatic pouch, *uterus masculinus*, or *sinus pocularis*, forms the atrophied remnant of the distal end of the genital cord, and is, of course, therefore, the homologue, in the male, of the vagina and uterus in the female.

Fig. 465.

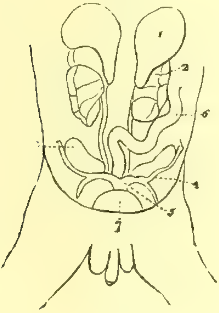


Fig. 466.

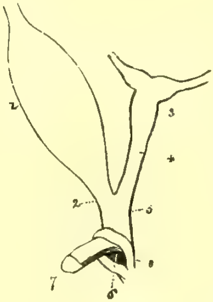


Fig. 467.

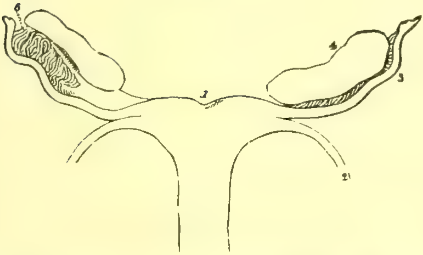
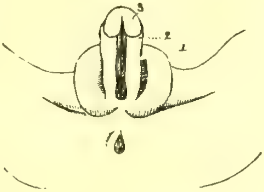


Fig. 468.



Urinary and generative organs of a human female embryo, measuring 3½ inches in length.

Fig. 465.—General view of these parts; 1, supra-renal capsules; 2, kidneys; 3, ovary; 4, Fallopian tube; 5, uterus; 6, intestine; 7, the bladder.
Fig. 466.—Bladder and Generative organs of the same embryo viewed from the side; *a*, the urinary bladder (at the upper part is a portion of the urachus); 2, urethra; 3, uterus (with two cornua); 4, vagina; 5, part as yet common to the vagina and urethra; 6, common orifice of the urinary and generative organs; 7, the clitoris.
Fig. 467.—Internal generative organs of the same embryo; 1, the uterus; 2, the round ligaments; 3, the Fallopian tubes (formed by the Müllerian ducts); 4, the ovaries; 5, the remains of the Wolffian bodies.
Fig. 468.—External generative organs of the same embryo; 1, the labia majora; 2, the nymphæ; 3, clitoris; 4, anus. (Müller).

The external parts of generation are at first the same in both sexes. The opening of the genito-urinary apparatus is, in both sexes, bounded by two folds of skin, whilst in front of it there is formed a penis-like body surmounted by a glans, and cleft or furrowed along its under surface. The borders of the furrows diverge posteriorly, running at the sides of the genito-urinary orifice internally to the cutaneous folds just mentioned (see figs. 465, 466, 467). In the female, this body becoming retracted, forms the clitoris, and the margins of the furrow on its under surface are converted into the nymphæ, or labia minora, the labia majora pudendæ being constituted by the great cutaneous folds. In the male fœtus, the margins of the furrow at the under surface of the penis unite at about the fourteenth week, and form that part of the urethra which is included in the penis. The large cutaneous folds form the scrotum, and later (in the eighth month of development), receive the testicles, which descend into them from the abdominal cavity. Sometimes the urethra is not closed, and the deformity called hypospadias then results. The appearance of hermaphroditism may, in these cases, be increased by the retention of the testes within the abdomen.

CHAPTER XXI.*

ON THE RELATION OF LIFE TO OTHER FORCES.

An enumeration of theories concerning the nature of life would be beside the purpose of the present chapter. They are interesting as marks of the way in which various minds have been influenced by the mystery which has always hung about vitality; their destruction is but another warning that any theory we can frame must be considered only a tie for connecting present facts, and one that must yield or break on any addition to the number which it is to bind together.

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[*] This chapter is a reprint, with some verbal alterations, of an essay contributed to *St. Bartholomew's Hospital Reports*, 1867, by W. Morrant Baker.

Before attention had been drawn to the mutual convertibility of the various so-called physical forces—heat, light, electricity, and others—and until it had been shown that these, like the matter through which they act, are limited in amount, and strictly measurable; that a given quantity of one force can produce a certain quantity of another and no more; that a given quantity of combustible material can produce only a given quantity of steam, and this again only so much motive power; it was natural that men's minds should be satisfied with the thought that vital force was some peculiar innate power, unlimited by matter, and altogether independent of structure and organisation. The comparison of life to a flame is probably as early as any thought about life at all. And so long as light and heat were thought to be inherent qualities of certain material which perished utterly in their production, it is not strange that life also should have been reckoned some strange spirit, pent up in the germ, expending itself in growth and development, and finally declining and perishing with the body which it had inhabited.

With the recognition, however, of a distinct correlation between the physical forces, came as a natural consequence a revolution of the commonly accepted theories concerning life also. The dictum, so long accepted, that life was essentially independent of physical force began to be questioned.

As it is well-nigh impossible to give a definition of life that shall be short, comprehensive, and intelligible, it will be best, perhaps, to take its chief manifestations, and see how far these seem to be dependent on other forces in nature, and how connected with them.

Life manifests itself by Birth, Growth, Development, Decline and Death; and an idea of life will most naturally arise by taking these events in succession, and studying them individually, and in relation to each other.

When the embryo in a seed awakes from that state, neither life nor death, which is called dormant vitality, and, bursting its envelopes, begins to grow up and develope, it may be said that there is a birth. And so, when the chick escapes from the egg, and when any living form is, as the phrase goes, brought into the world. In each case, however, birth is not the beginning of life, but only the continuation of it under different conditions. To understand the beginning of life in any individual, whether plant or animal, existence must be traced somewhat further back, and in this way an idea gained concerning the nature of the germ, the development of which is to issue in birth.

The germ may be defined as that portion of the parent which is set apart with power to grow up into the likeness of the being from which it has been derived.

The manner in which the germ is separated from the parent does not here concern us. It belongs to the special subject of generation. Neither need we consider apart from others those modes of propagation, as fission and gemmation, which differ more apparently than really from the ordinary process typified in the formation of the seed or ovum. In every case alike, a new individual plant or animal is a portion of its parent: it may be a mere outgrowth or bud, which, if separated, can maintain an independent existence; it may be not an outgrowth but simply a portion of the parent's structure, which has been naturally or artificially cut off, as in the spontaneous or artificial cleaving of a polype; it may be the embryo of a seed or ovum, as in those cases in which the process of multiplication of different organs has reached the point of separation of the individual more or less completely into two sexes, the mutual conjugation of a portion of each of which, the sperm-cell and the germ-cell, is necessary for the production of a new being. We are so accustomed to regard the conjugation of the two sexes as necessary for what is called generation, that we are apt to forget that it is only gradually in the upward progress of development of the vegetable and animal kingdoms, that those portions of organised matter which are to produce new beings are allotted to two separate individuals. In the least developed forms of life, almost any part of the body is capable of assuming the characters of a separate individual; and propagation, therefore, occurs by fission or gemmation in some form or other. Then, in beings a little higher in rank, only a special part of the body can become a separate being, and only by conjugation with another special part. Still, there is but one parent; and this hermaphrodite-form of generation is the rule in the vegetable and least developed portion of the animal kingdom. At last, in all animals but the lowest, and in some plants, the portions of organised structure specialised for development after their mutual union into a new individual, are found on two distinct beings, which we call respectively male and female.

The old idea concerning the power of growth resident in the germ of the new being, thus formed in various ways, was expressed by saying that a store of dormant vitality was laid up in it, and that so long as no decomposition ensued, this was capable of manifesting itself and becoming active under the influence of certain external conditions. Thus, the dormant force supposed to be present in the seed or the egg was assumed to be the primary agent in effecting development and growth, and to continue in action during the whole term of life of the living being, animal or vegetable, in which it was said to reside. The influence of external forces—heat, light, and others—was noticed and appreciated; but these were thought to have no other connection with vital force than that in some way or other they called it into action, and that to some extent it was dependent on them for its continuance. They were not supposed to be correlated with it in any other sense than this.

Now, however, we are obliged to modify considerably our notions and with them our terms of expression, when describing the origin and birth of a new being.

To take, as before, the simplest case—a seed or egg. We must suppose that the heat, which in conjunction with moisture is necessary for the development of those changes which issue in the growth of a new plant or animal, is not simply an agent which so stimulates the dormant vitality in the seed or egg as to make it cause growth, but it is a force, which is itself transformed into chemical and vital power. The embryo in the seed or egg is a part which can transform heat into vital force, this term being a convenient one wherewith to express the power which particular structures possess of growing, developing, and performing other actions which we call vital.*

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* The term "vital force" is here employed for the sake of brevity. Whether it is strictly admissible will be discussed hereafter.

The general term *force* is used as synonymous with what is now often termed *energy*.

Of course the embryo can grow only by taking up fresh material and incorporating it with its own structure, and therefore it is surrounded in the seed or ovum with matter sufficient for nutrition until it can obtain fresh supplies from without. The absorption of this nutrient matter involves an expenditure of force of some kind or other, inasmuch as it implies the raising of simple to more complicated forms. Hence the necessity for heat or some other power before the embryo can exhibit any sign of life. It would be quite as impossible for the germ to begin life without external force as without a supply of nutrient matter. Without the force wherewith to take it, the matter would be useless. The heat, therefore, which in conjunction with moisture is necessary for the beginning of life, is partly expended as chemical power, which causes certain modifications in the nutrient material surrounding the embryo, *e.g.*, the transformation of starch into sugar in the act of germination; partly, it is transformed by the germ itself into vital force, whereby the germ is enabled to take up the nutrient material presented to it, and arrange it in forms characteristic of life. Thus the force is expended, and thus life begins—when a particle of organised matter, which has itself been produced by the agency of life, begins to transform external force into vital force, or in other words into a power by which it is enabled to grow and develop. This is the true beginning of life. The time of birth is but a particular period in the process of development at which the germ, having arrived at a fit state for a more independent existence, steps forth into the outer world.

The term "dormant vitality," must be taken to mean simply the existence of organised matter with the *capacity* of transforming heat or other force into vital or growing power, when this force is applied to it under proper conditions.

The state of dormant vitality is like that of an empty voltaic battery, or a steam-engine in which the fuel is not yet lighted. In the former case no electric current passes, because no chemical action is going on. There is no transformation into electric force, because there is no chemical force to be transformed. Yet, we do not say, in this instance, that there is a store of electricity laid up in a dormant state in the battery; neither do we say that a store of motion is laid up in the steam-engine. And there is as little reason for saying there is a store of vitality in a dormant seed or ovum.

Next to the beginning of life, we have to consider how far its continuance by growth and development is dependent on external force and to what extent correlated with it.

Mere growth is not a special peculiarity of living beings. A crystal, if placed in a proper solution, will increase in size and preserve its own characteristic outline; and even if it be injured, the flaw can be in part or wholly repaired. The manner of its growth, however, is very different from that of a living being, and the process as it occurs in the latter will be made more evident by a comparison of the two cases. The increase of a crystal takes place simply by the laying of material on the surface only, and is unaccompanied by any interstitial change. This is, however, but an accidental difference. A much greater one is to be found in the fact that with the growth of a crystal there is no decay at the same time, and proceeding with it side by side. Since there is no life there is no need of death—the one being a condition consequent on the other. During the whole life of a living being, on the other hand, there is unceasing change. At different periods of existence the relation between waste and repair is of course different. In early life the addition is greater than the loss, and so there is growth; the reconstructed part is better than it was before, and so there is development. In the decline of life, on the contrary, the renewal is less than the destruction, and instead of development there is degeneration. But at no time is there perfect rest or stability.

It must not be supposed, therefore, that life consists in the capability of resisting decay. Formerly, when but little or nothing was known about the laws which regulate the existence of living beings, it was reasonable enough to entertain such an idea; and, indeed, life was thought to be, essentially, a mysterious power counteracting that tendency to decay which is so evident when life has departed. Now, we know that so far from life preventing decomposition, it is absolutely dependent upon it for all its manifestations.

The reason of this is very evident. Apart from the doctrine of correlation of force, it is of course plain that tissues which do work must sooner or later wear out if not constantly supplied with nourishment; and the need of a continual supply of food, on the one hand, and, on the other, the constant excretion of matter which, having evidently discharged what was required of it, was fit only to be cast out, taught this fact very plainly. But although, to a certain extent, the dependence of vital power on supplies of matter from without was recognised and appreciated, the true relation between the demand and supply was not until recently thoroughly grasped. The doctrine of the correlation of vital with other forces was not understood.

To make this more plain, it will be well to take an instance of transformation of force more commonly known and appreciated. In the steam-engine a certain amount of force is exhibited as motion, and the immediate agent in the production of this is steam, which again is the result of a certain expenditure of heat. Thus, heat is in this instance said to be transformed into motion, or, in other language, one—molecular—mode of motion, heat, is made to express itself by another—mechanical—mode, ordinary movement. But the heat which produced the vapour is itself the product of the combustion of fuel, or, in other words, it is the correlated expression of another force—chemical, namely, that affinity of carbon and hydrogen for oxygen which is satisfied in the act of combustion. Again, the production of light and heat by the burning of coal and wood is only the giving out again of that heat and light of the sun which were used in their production. For, as it need scarcely be said, it is only by means of these solar forces that the leaves of plants can decompose carbonic acid, &c., and thereby provide material for the construction of woody tissue. Thus, coal and wood being products of the expenditure of force, must be taken to represent a certain amount of power; and, according to the law of the correlation of forces, must be capable of yielding, in some shape or other, just so much as was exercised in their formation. The amount of force requisite for rending asunder the elements of carbonic acid is exactly that amount which will again be manifested when they clash together again.

The sun, then, really, is the prime agent in the movement of the steam-engine, as it is indeed in the production of nearly all the power manifested on this globe. In this particular instance, speaking roughly, its light and heat are manifested successively as vital and chemical force in the growth of plants, as heat and light again in the burning fuel, and lastly by the piston and wheels of the engine as motive power. We may use the term transformation of force if we will, or say that throughout the cycle of changes there is but one force variously manifesting itself. It matters not, so that we keep clearly in view the notion that all force, so far at least as our present knowledge extends, is but a representative, it may be in the same form or another, of some previous force, and incapable like matter, of being created afresh, except by the Creator. Much of our knowledge on this subject is of course confined to ideas, and governed by the words with which we are compelled to express them, rather than to actual things or facts; and probably the term force will soon lose the signification which we now attach to it. What is now known, however, about the relation of one force to another, is not sufficient for the complete destruction of old ideas; and, therefore, in applying the examples of transformation of physical force to the explanation of vital phenomena, we are compelled still to use a vocabulary which was framed for expressing many notions now obsolete.

The dependence of the lowest kind of vital existence on external force, and the manner in which this is used as a means whereby life is manifested, have been incidentally referred to more than once when describing the origin of vegetable tissues. The main functions of the vegetable kingdom are construction, and the perpetuation of the race; and the use which is made of external physical force is more simple than in animals. The transformation indeed which is effected, while much less mysterious than in the latter instance, forms an interesting link between animal and crystalline growth.

The decomposition of carbonic acid or ammonia by the leaves of plants may be compared to that of water by a galvanic current. In both cases a force is applied through a special material medium, and the result is a separation of the elements of which each compound is formed. On the return of the elements to their original state of union, there will be the return also in some form or other of the force which was used to separate them. Vegetable growth, moreover, with which we are now specially concerned, resembles somewhat the increase of unorganised matter. The accidental difference of its being in one case superficial, and in the other interstitial, is but little marked in the process as it occurs in the more permanent parts of vegetable tissues. The layers of lignine are in their arrangement nearly as simple as those of a crystal, and almost or quite as lifeless. After their deposition, moreover, they undergo no further change than that caused by the addition of fresh matter, and hence they are not instances of that ceaseless waste and repair which have been referred to as so characteristic of the higher forms of living tissue. There is, however, no contradiction here of the axiom, that where there is life there is constant change. Those parts of a vegetable organism in which active life is going on are subject, like the tissues of animals, to constant destruction and renewal. But, in the more permanent parts, life ceases with deposition and construction. Addition of fresh matter may occur, and so may decay also of that which is already laid down, but the two processes are not related to each other, and not, as in living parts, inter-dependent. Hence the change is not a vital one.

The acquirement in growth, moreover, of a definite shape in the case of a tree, is no more admirable or mysterious than the production of a crystal. That chloride of sodium should naturally assume the form of a cube is as inexplicable as that an acorn should grow into an oak, or an ovum into a man. When we learn the cause in the one case we shall probably in the other also.

There is nothing, therefore, in the products of life's more simple forms that need make us start at the notion of their being the products of only a special transformation of ordinary physical force, and we cannot doubt that the growth and development of animals obey the same general laws that govern the formation of plants. The connecting links between them are too numerous for the acceptance of any other supposition. Both kingdoms alike are expressions of vital force, which is itself but a term for a special transformation of ordinary physical force. The mode of the transformation is, indeed, mysterious, but so is that of heat into light, or of either into mechanical motion or chemical affinity. All forms of life are as absolutely dependent on external physical force as a fire is dependent for its continuance on a supply of fuel; and there is as much reason to be certain that vital force is an expression or representation of the physical forces, especially heat and light, as that these are the correlates of some force or other which has acted or is acting on the substances which, as we say, produce them.

In the tissues of plants, as just said, there is but little change, except such as is produced by additions of fresh matter. That which is once deposited alters but little; or, if the part be transient and easily perishable, the alteration is only or chiefly one produced by the ordinary process of decay. Little or no force is manifested; or, if it be, it is only the heat of the slow oxidation whereby the structure again returns to inorganic shape. There is no special transformation of force to which the term vital can be applied. With construction the chief end of vegetable existence has been attained, and the tissue formed represents a store of force to be used, but not by the being which laid it up. The labours of the vegetable world are not for itself but for animals. The power laid up by the one is spent by the other. Hence the reason that the constant change, which is so great a character of life, is comparatively but little marked in plants. It is present, but only in living portions of the organism, and in these it is but limited. In a tree the greater part of the tissues may be considered dead; the only change they suffer is that fresh matter is piled on to them. They are not the seat of any transformation of force, and therefore, although their existence is the result of living action, they do not themselves live. Force is, so, to speak, laid up in them, but they do not themselves spend it. Those portions of a vegetable organism which are doing active vital work—which are using the sun's light and heat, as a means whereby to prepare building material, are, however, the seat of unceasing change. Their existence as living tissue depends upon this fact—upon their capability of perishing and being renewed.

And this leads to the answer to the question, What is the cause of the constant change which occurs in the living parts of animals and vegetables, which is so invariable an accompaniment of life, that we refuse the title of "living" to parts not attended by it? It is because all manifestations of life are exhibitions of power, and as no power can be originated by us: as, according to the doctrine of correlation of force, all power is but the representative of some previous force in the same or another form, so, for its production, there must be expenditure and change somewhere or other. For the vital actions of plants the light and heat of the sun are nearly or quite sufficient, and there is no need of expenditure of that store of force which is laid up in themselves; but with animals the case is different. They cannot directly transform the solar forces into vital power; they must seek it elsewhere. The great use of the vegetable kingdom is therefore to store up power in such a form that it can be used by animals; that so, when in the bodies of the latter, vegetable organised material returns to an inorganic condition, it may give out force in such a manner that it can be transformed by animal tissues, and manifested variously by them as vital power.

Hence, then, we must consider the waste and repair attendant on living growth, and development as something more than these words, taken by themselves, imply. The waste is the return to a lower from a higher form of matter; and, in the fall, force is manifested. This force, when specially transformed by organised tissues, we call vital. In the repair, force is laid up. The analogy with ordinary transmutations of physical force is perfect. By the expenditure of heat in a particular manner a weight can be raised. By its fall heat is returned. The molecular motion is but the expression in another form of the mechanical. So with life. There is constant renewal and decay, because it is only so that vital activity can take place. The renewal must be something more than replacement, however, as the decay must be more than simple mechanical loss. The idea of life must include both storing up of force, and its transformation in the expenditure.

Hence we must be careful not to confound the mere preservation of individual form under the circumstances of concurrent waste and repair, with the essential nature of vitality.

Life, in its simplest form, has been happily expressed by Savory as a state of dynamical equilibrium, since one of its most characteristic features is continual decay, yet with maintenance for the individual by equally constant repair. Since, then, in the preservation of the equilibrium there is ceaseless change, it is not static equilibrium but dynamical.

Care must be taken, however, not to accept the term in too strict a sense, and not to confound that which is but a necessary attendant on life with life itself. For, indeed, strictly, there is no preservation of equilibrium during life. Each vital act is an advance towards death. We are accustomed to make use of the terms growth and development in the sense of progress in one direction, and the words decline and decay with an opposite signification, as if, like the ebb of the tide, there were after maturity a reversal of life's current. But, to use an equally old comparison, life is really a journey always in one direction. It is an ascent, more and more gradual as the summit is approached, so gradual that it is impossible to say when development ends and decline begins. But the descent is on the other side. There is no perfect equilibrium, no halting, no turning back.

The term, therefore, must be used with only a limited signification. There is preservation of the individual, yet, although it may seem a paradox, not of the same individual. A man at one period of his life may retain not a particle of the matter of which formerly he was composed. The preservation of a living being during growth and development is more comparable, indeed, to that of a nation, than of an individual as the term is popularly understood. The elements of which it is made up fulfil a certain work the traditions of which were handed down from their predecessors, and then pass away, leaving the same legacy to those that follow them. The individuality is preserved, but, like all things handed down by tradition, its fashion changes, until at last, perhaps, scarce any likeness to the original can be discovered. Or, as it sometimes happens, the alterations by time are so small that we wonder, not at the change, but the want of it. Yet, in both cases alike, the individuality is preserved, not by the same individual elements throughout, but by a succession of them.

Again, concurrent waste and repair do not imply of necessity the existence of life. It is true that living beings are the chief instances of the simultaneous occurrence of these things. But this happens only because the conditions under which the functions of life are discharged are the principal examples of the necessity for this unceasing and mingled destruction and renewal. They are the chief, but not the only instances of this curious conjunction.

A theoretical case will make this plain. Suppose an instance of some permanent structure, say a marble statue. If we imagine it to be placed under some external conditions by which each particle of its substance should waste and be replaced, yet with maintenance of its original size and shape, we obtain no idea of life. There is waste and renewal, with preservation of the individual form, but no vitality. And the reason is plain. With the waste of a substance like carbonate of calcium whose attractions are satisfied, there would be no evolution of force; and even if there were, no structure is present with the power to transform or manifest anew any power which might be evolved. With the repair, likewise, there would be no storing of force. The part used to make good the loss is not different from that which disappeared. There is therefore neither storing of force, nor its transformation, nor its expenditure; and therefore there is no life.

But real examples of the preservation of an individual substance under the circumstances of constant loss and renewal, may be found, yet without any semblance in them of life.

Chemistry, perhaps, affords some of the neatest and best examples of this. One, suggested by Shepard, seems particularly apposite. It is the case of trioxide of nitrogen (N_2O_3) in the preparation of sulphuric acid. The gas from which this acid is obtained is sulphur dioxide, and the addition of an equivalent of oxygen and the combination of the resulting sulphur trioxide (SO_3) with water (H_2O) is all that is required. Thus:

$$\begin{array}{ccccccc} SO_2 & + & O & + & H_2O & = & H_2SO_4 \\ \text{Sulph. dioxide} & : & \text{Oxygen} & : & \text{Water} & = & \text{Sulphuric Acid.} \end{array}$$

Sulphur dioxide, however, cannot take the necessary oxygen directly from the atmosphere, but it can abstract it from trioxide of nitrogen (N_2O_3), when the two gases are mingled. The trioxide, accordingly, by continually giving up an equivalent of oxygen to an equivalent of sulphur dioxide, causes the formation of sulphuric acid, at the same time that it retains its composition by continually absorbing a fresh quantity of oxygen from the atmosphere.

In this instance, then, there is constant waste and repair, yet without life. And here an objection cannot be raised, as it might be to the preceding example, that both the destruction and repair come from without, and are not dependent on any inherent qualities of the substance with which they have to do. The waste and renewal in the last-named example are strictly dependent on the qualities of the chemical compound which is subject to them. It has but to be placed in appropriate conditions, and destruction and repair will continue indefinitely. Force, too, is manifested, but there is nothing present which can transform it into vital shape, and so there is no life.

Hence, our notion of the constant decay which, together with repair, takes place throughout life, must be not confined to any simply mechanical act. It must include the idea, as before said, of laying up of force, and its expenditure—its transformation too, in the act of being expended.

The growth, then, of an animal or vegetable, implies the expenditure of physical force by organized tissue, as a means whereby fresh matter is added to and incorporated with that already existing. In the case of the plant the force used, transformed, and stored up, is almost entirely derived from external sources; the material used is inorganic. The result is a tissue which is not intended for expenditure by the individual which has accumulated it. The force expended in growth by animals, on the other hand, cannot be obtained directly from without. For them a supply of force is necessary in the shape of food derived directly or indirectly from the vegetable kingdom. Part of this force-containing food is expended as fuel for the production of power; and the latter is used as a means wherewith to elaborate another portion of the food, and incorporate it as animal structure. Unlike vegetable structure, however, animal tissues are the seat of constant change, because their object is not the storing up of power, but its expenditure; so there must be constant waste; and if this happen, then for the continuance of life there must be equally constant repair. But, as before said, in early life the repair surpasses the loss, and so there is growth. The part repaired is better than before the loss, and thus there is development.

The definite limit which has been imposed on the duration of life has been already incidentally referred to. Like birth, growth, and development, it belongs essentially to living beings only. Dead structures and those which have never lived are subject to change and destruction, but decay in them is uncertain in its beginning and continuance. It depends almost entirely on external conditions, and differs altogether from the decline of life.

The decline and death of living beings are as definite in their occurrence as growth and development. Like these they may be hastened or stayed, especially in the lower forms of life, by various influences from without; but the putting off of decline must be the putting off also of so much life; and, apart from disease, the reverse is true also. A living being starts on its career with a certain amount of work to do—various infinitely in different individuals, but for each well-defined. In the lowest members of both the animal and vegetable creation the progress of life in any given time seems to depend almost entirely on external circumstances; and at first sight it seems almost as if these lowly-formed organisms were but the sport of the surrounding elements. But it is only so in appearance, not in reality. Each act of their life is so much expended of the time and work allotted to them; and if, from absence of those surrounding conditions under which alone life is possible, their vitality is stayed for a time, it again proceeds on the renewal of the necessary conditions, from that point which it had already attained. The amount of life to be manifested by any given individual is the same, whether it takes a day or a year for its expenditure. Life may be of course at any moment interrupted altogether by disease and death. But supposing it, in any individual organism, to run its natural course, it will attain but the same goal, whatever be its rate of movement. Decline and death, therefore, are but the natural terminations of life; they form part of the conditions on which vital action begins; they are the end towards which it naturally tends. Death, not by disease or injury, is not so much a violent interruption of the course of life, as the attainment of a distant object which was in view from the commencement.

In the period of decline, as during growth, life consists in continued manifestations of transformed physical force; and there is of necessity the same series of changes by which the individual, though bit by bit perishing, yet by constant renewal retains its entity. The difference, as has been more than once said, is in the comparative extent of the loss and reproduction. In decline there is not perfect replacement of that which is lost. Repair becomes less and less perfect. It does not of necessity happen that there is any decrease of the quantity of material added in the place of that which disappears. But although the quantity may not be lessened, and may indeed absolutely increase, it is not perfect as material for repair, and although there may be no wasting, there is degeneration.

No definite period can be assigned as existing between the end of development and the beginning of decline, and chiefly because the two processes go on side by side in different parts of the same organism. The transition as a whole is therefore too gradual for appreciation. But, after some time, all parts alike share in the tendency to degeneration; until at length, being no longer able to subdue external force to vital shape, they die; and the elements of which they are composed simply employ what remnant of power, in the shape of chemical affinity, is still left in them, as a means whereby they may go back to the inorganic world. Of course the same process happens constantly during life; but in death the place of the departing elements is not taken by others.

Here, then, a sharp boundary line is drawn where one kind of action stops and the other begins; where physical force ceases to be manifested except as physical force, and where no further vital transformation takes place, or can in the body ever do so. For the notion of death must include the idea of impossibility of revival, as a distinction from that state of what is called "dormant vitality," in which, although there is no life, there is capability of living. Hence the explanation of the difference between the effect of appliance of external force in the two cases. Take, for examples, the fertile but not yet living egg, and the barren or dead one. Every application of force to the one must excite movement in the direction of development; the force, if used at all, is transformed by the germ into vital energy, or the power by which it can gather up and elaborate the materials for nutrition by which it is surrounded. Hence its freedom throughout the brooding time from putrefaction. In the other instance, the appliance of force excites only degeneration; if transformed at all, it is only into chemical force, whereby the progress of destruction is hastened; hence it soon rots. To the one, heat is the signal for development, to the other for decay. By one it is taken up and manifested anew, and in a higher form; to the other it gives the impetus for a still quicker fall.

Life, then, does not stand alone. It is but a special manifestation of transformed force. "But if this be so," it may be said—"if the resemblance of life to other forces be great, are not the differences still greater?"

At the first glance, the distinctions between living organised tissue and inorganic matter seem so great that the difficulty is in finding a likeness. And there is no doubt that these wide differences in both outward configuration and intimate composition have been mainly the causes of the delay in the recognition of the claims of life to a place among other forces. And reasonably enough. For the notion that a plant or an animal can have any kind of relationship in the discharge of its functions to a galvanic battery or a steam engine is sufficiently startling to the most credulous. But so it has been proved to be.

Among the distinctions between living and unorganised matter, that which includes differences in structure and proximate chemical composition has been always reckoned a great one. The very terms organic and inorganic were, until quite recently, almost synonymous with those which implied the influence of life and the want of it. The science of chemistry, however, is a great leveller of artificial distinctions, and many complex substances which, it was supposed, could not be formed without the agency of life can be now made directly from their elements or from very simple combinations of these. The number of complex substances so formed artificially is constantly increasing; and there seems to be no reason for doubting that even such as albumin, gelatin, and the like, will be ultimately produced without the intermediation of living structure.

The formation of the latter, such an organised structure for instance as a cell or a muscular fibre, is a different thing altogether. There is at present no reason for believing that such will ever be formed by artificial means; and, therefore, among the peculiarities of living force-transforming agents, must be reckoned as a great and essential one, a special intimate structure, apart from mere ultimate or proximate chemical composition, to which there is no close likeness in any artificial apparatus, even the most complicated. This is the real distinction, as regards composition, between a living tissue and an inorganic machine; namely, the difference between the structural arrangement by which force is transformed and manifested anew. The fact that one agent for transforming force is made of albumen or the like, and another of zinc or iron, is a great distinction, but not so essential or fundamental an one as the difference in mechanical structure and arrangement.

In proceeding to consider the difference between what may be called the transformation-products of living tissue, and of an artificial machine, it will be well to take one of the simple cases first —the production of mechanical motion; and especially because it is so common in both.

In one we can trace the transformation. We know, as a fact, that heat produces expansion (steam), and by constructing an apparatus which provides for the application of the expansive power in opposite directions alternately, or by alternating contraction with expansion, we are able to produce motion so as to subserve an infinite variety of purposes. For the continuance of the motion there must be a constant supply of heat, and therefore of fuel.

In the production of mechanical motion by the alternate contractions of muscular fibres we cannot trace the transformation of force at all. We know that the constant supply of force is as necessary in this instance as in the other; and that the food which an animal absorbs is as necessary as the fuel in the former case, and is analogous with it in function. In what exact relation, however, the latent force in the food stands to the movement in the fibre, we are at present quite ignorant. That in some way or other, however, the transformation occurs, we may feel quite certain.

There is another distinction between the two exhibitions of force which must be noticed. It has been universally believed, almost up to the present time, that in the production of living force the result is obtained by an exactly corresponding waste of the tissue which produces it; that, for instance, the power of each contraction of a muscle is the exact equivalent of the force produced by the more or less complete descent of so much muscular substance to inorganic, or less complex organic shape; in other words,—that the immediate fuel which an animal requires for the production of force is derived from its own substance; and that the food taken must first be appropriated by, and enter into the very formation of living tissue before its latent force can be transformed and manifested as vital power. And here, it might be said, is a great distinction between a living structure and a simply mechanical arrangement such as that which has been used for comparison; the fuel which is analogous to the food of a plant or animal does not, as in the case of the latter, first form part of the machine which transforms its latent energy into another variety of power.

We are not, at present, in a position to deny that this is a real and great distinction between the two cases; but modern investigations in more than one direction lead to the belief that we must hesitate before allowing such a difference to be an universal or essential one. The experiments referred to seem conclusive in regard to the production of muscular power in greater amount than can be accounted for by the products of muscular waste excreted; and it may be said with justice, that there is no intrinsic improbability in the supposed occurrence of transformation of force, apart from equivalent nutrition and subsequent destruction of the transforming agent. Argument from analogy, indeed, would be in favour of the more recent theory as the likelier of the two.

Whatever may be the result of investigations concerning the relation of waste of living tissue to the production of power, there can be no doubt, of course, that the changes in any part which is the seat of vital action must be considerable, not only from what may be called "wear and tear," but, also, on account of the great instability of all organised structures. Between such waste as this, however, and that of an inorganic machine there is only the difference in degree, arising necessarily from diversity of structure, of elemental arrangement, and so forth. But the repair in the two cases is different. The capability of reconstruction in a living body is an inherent quality like that which causes growth in a special shape or to a certain degree. At present we know nothing really of its nature, and we are therefore compelled to express the fact of its existence by such terms as "inherent power," "individual endowment," and the like, and wait for more facts which may ultimately explain it. This special quality is not indeed one of living things alone. The repair of a crystal in definite shape is equally an "individual endowment," or "inherent peculiarity," of the nature of which we are equally ignorant. In the case, however, of an inorganic machine there is nothing of the sort, not even as in a crystal. Faults of structure must be repaired by some means entirely from without. And as our notion of a living being, say a horse, would be entirely altered if flaws in his composition were repaired by external means only; so, in like manner, would our idea of the nature of a steam-engine be completely changed had it the power of absorbing and using part of its fuel as matter wherewith to repair any ordinary injury it might sustain.

It is this ignorance of the nature of such an act as reconstruction which causes it to be said, with apparent reason, that so long as the term "vital force" is used, so long do we beg the question at issue—What is the nature of life? A little consideration, however, will show that the justice of this criticism depends on the manner in which the word "vital" is used. If by it we intend to express an idea of something which arises in a totally different manner from other forces—something which, we know not how, depends on a special innate quality of living beings, and owns no dependence on ordinary physical force, but is simply stimulated by it, and has no correlation with it—then, indeed, it would be just to say that the whole matter is merely shelved if we retain the term "vital force."

But if a distinct correlation be recognised between ordinary physical force and that which in various shapes is manifested by living beings; if it be granted that every act—say, for example, of a brain or muscle—is the exactly correlated expression of a certain quantity of force latent in the food with which an animal is nourished; and that the force produced either in the shape of thought or movement is but the transformed expression of external force, and can no more originate in a living organ without supplies of force from without, than can that organ itself be formed or nourished without supplies of matter;—if these facts be recognised, then the term used in speaking of the powers exercised by a living being is not of very much consequence. We have as much right to use the term "vital" as the words galvanic and chemical. All alike are but the expressions of our ignorance concerning the nature of that power of which all that we call "forces" are various manifestations. The difference is in the apparatus by which the force is transformed.

It is with this meaning that, for the present, the term "vital force" may still be retained when we wish shortly to name that combination of energies which we call life. For, exult as we may at the discovery of the transformation of physical force into vital action, we must acknowledge not only that, with the exception of some slight details, we are utterly ignorant of the process by which the transformation is effected; but, as well, that the result is in many ways altogether different from that of any other force with which we are acquainted.

It is impossible to define in what respects, exactly, vital force differs from any other. For while some of its manifestations are identical with ordinary physical force, others have no parallel whatsoever. And it is this mixed nature which has hitherto baffled all attempts to define life, and, like a Will-o'-the-wisp, has led us floundering on through one definition after another only to escape our grasp and show our impotence to seize it.

In examining, therefore, the distinctions between the products of transformations by a living and by an inorganic machine, we have first to recognise the fact, that while in some cases the difference is so faint as to be nearly or quite imperceptible, in others there seems not a trace of resemblance to be discovered.

In discussing the nature of life's manifestations—birth, growth, development, and decline—the differences which exist between them and other processes more or less resembling them, but not dependent on life, have been already briefly considered and need not be here repeated. It may be well, however, to sum up very shortly the particulars in which life as a manifestation of force differs from all others.

The mere acquirement of a certain shape by growth is not a peculiarity of life. But the power of developing into so composite a mass even as a vegetable cell is a property possessed by an organised being only. In the increase of inorganic matter there is no development. The minutest crystal of any given salt has exactly the same shape and intimate structure as the largest. With the growth there is no development. There is increase of size with retention of the original shape, but nothing more. And if we consider the matter a little we shall see a reason for this. In all force-transformers, whether living or inorganic, with but few exceptions—and these are, probably, apparent only—something more is required than homogeneity of structure. There seems to be a need for some mutual dependence of one part on another, some distinction of qualities, which cannot happen when all portions are exactly alike. And here lies the resemblance between a living being and an artificial machine. Both are developments, and depend for their power of transforming force on that mutual relation of the several parts of their structure which we call organisation. But here, also, lies a great difference. The development of a living being is due to an inherent tendency to assume a certain form; about which tendency we know absolutely nothing. We recognise the fact, and that is all. The development of an inorganic machine—say an electrical apparatus—is not due to any inherent or individual property. It is the result of a power entirely from without; and we know exactly how to construct it.

Here, then, again, we recognise the compound nature of a living being. In structure it is altgether different from a crystal—in inherent capacity of growth into definite shape it resembles it. Again, in the fact of its organisation it resembles a machine made by man: in capacity of growth it entirely differs from it. In regard, therefore, to structure, growth, and development, it has combined in itself qualities which in all other things are more or less completely separated.

That modification of ordinary growth and development called generation, which consists in the natural production and separation of a portion of organised structure, with power itself to transform force so as therewith to build up an organism like the being from which it was thrown off, is another distinctive peculiarity of a living being. We know of nothing like it in the inorganic world. And the distinction is the greater because it is the fulfilment of a purpose, towards which life is evidently, from its very beginning, constantly tending. It is as natural a destiny to separate parts which shall form independent beings as it is to develop a limb. Hence it is another instance of that carrying out of certain projects, from the very beginning in view, which is so characteristic of things living and of no other.

It is especially in the discharge of what are called the animal functions that we see vital force most strangely manifested. It is true that one of the actions included in this term—namely mechanical movement—although one of the most striking, is by no means a distinctive one. For it must be remembered that one of the commonest transformations of physical force with which we are acquainted is that of heat into mechanical motion, and that this may be effected by an apparatus having itself nothing whatever to do with life. The peculiarity of the manifestation in an animal or vegetable is that of the organ by which it is effected, and the manner in which the transformation takes place, not in the ultimate result. The mere fact of an animal's possessing capability of movement is not more wonderful than the possession of a similar property by a steam engine. In both cases alike, the motion is the correlative expression of force latent in the food and fuel respectively; but in one case we can trace the transformation in the arrangement of parts, in the other we cannot.

The consideration of the products of the transformation of force effected by the nervous system would lead far beyond the limits of the present chapter. But although the relation of mind to matter is so little known that it is impossible to speak with any freedom concerning such correlative expressions of physical force as thought and nerve-products, still it cannot be doubted that they are as much the results of transformation of force as the mechanical motion caused by the contraction of a muscle. But here the mystery reaches its climax. We neither know how the change is effected, nor the nature of the product, nor its analogies with other forces. It is therefore better, for the present, to confess our ignorance, than, with the knowledge which we have lately gained, to build up rash theories, serving only to cause that confusion which is worse than error.

It may be said, with perfect justice, that even if the foregoing conclusions be accepted, namely, that all manifestations of force by living beings are correlative expressions of ordinary physical force, still the argument is based on the assumption of the existence of the apparatus which we call living organised matter, with power not only to use external force for its own use in growth, development, and other vital manifestations, but for that modification of these powers which consists in the separation of a part that shall grow up into the likeness of its parent, and thus continue the race. We are therefore, it may be added, as far as ever from any explanation of the origin of life. This is of course quite true. The object of the present chapter, however, is only to deal with the relations of life, as it now exists, to other forces. The manner of creation of the various kinds of organised matter, and the source of those qualities, belonging to it, which from our ignorance we call inherent, are different questions altogether.

To say that of necessity the power to form living organised matter will never be vouchsafed to us, that it is only a mere materialist who would believe in such a possibility, seems almost as absurd as the statement that such inquiries lead of necessity to the denial of any higher power than that which in various forms is manifested as "force," on this small portion of the universe. It is almost as absurd, but not quite. For, surely, he who recognises the doctrine of the mutual convertibility of all forces, vital and physical, who believes in their unity and imperishableness, should be the last to doubt the existence of an all-powerful Being, of whose will they are but the various correlative expressions; from whom they all come; to whom they return.

APPENDIX.

The Chemical Basis of the Human Body.

Of the sixty-four known chemical elements no less than seventeen have been found, in larger or smaller quantities, to form the chemical basis of the animal body.

The substances occurring in largest quantities are the non-metallic elements, Oxygen, Carbon, Hydrogen, and Nitrogen—oxygen and carbon making up altogether about 85 per cent. of the whole. The most abundant of the metallic elements are Calcium, Sodium, and Potassium.

The following table represents the relative proportion of the various elements.—(Marshall).

Oxygen	72·0
Carbon	13·5
Hydrogen	9·1
Nitrogen	2·5
Calcium	1·3
Phosphorus	1·15
Sulphur	·1476
Sodium	·1
Chlorine	·085
Fluorine	·08
Potassium	·026
Iron	·01
Magnesium	·0012
Silicon	·0002
(Traces of copper, lead, and aluminium)	
	100·

Compounds.—The elementary substances above-mentioned seldom occur free or uncombined in the animal body; but are nearly always united among themselves in various numbers, and in variable proportions to form "*compounds.*" Several elements have, however, been detected in small amount free; traces of uncombined *Oxygen* and *Nitrogen* have been found in the blood, and of *Hydrogen* as well as of *Oxygen* and *Nitrogen* in the intestinal canal.

Organic and Inorganic Compounds.—It was formerly thought that the more complex compounds built up by the animal or vegetable *organism* were peculiar, and could not be made artificially by chemists from their elements, and under this idea they were formed into a distinct class, termed *organic.* This idea has been given up, but the name is still in use, with a different signification. The term *organic* is now applied simply to the compounds of the element Carbon, irrespective of their complexity; chemists having found that these compounds are so numerous and important, and that they include all those to which the term *organic* was in former times exclusively given.

Characteristics of Organic Compounds.—The animal organic compounds are characterized as a rule by their *complexity*, for, in the first place many elements enter into their composition, thereby distinguishing them from bodies such as water (H_2O), hydrochloric acid (HCl), and ammonia (NH_3), which may be taken as types of inorganic compounds. And again, because many atoms of the same element occur in each molecule. This latter fact no doubt explains also the reason of the *instability* of organic compounds.

Another great cause of the instability arises from the fact that many such compounds contain the element Nitrogen, which may be called negative or undecided in its affinities, and may be easily separated from combination with other elements.

Animal tissues, containing as they do these organic nitrogenous compounds, are extremely prone to undergo chemical decomposition, and this is especially the case since they also contain a large quantity of water, a condition most favourable for the breaking up of such substances. It is from this fact that in the consideration of the chemical basis of the body we meet with an extremely large number of decomposition products.

In treating of the various substances found in the animal organism it is convenient to adopt the division into—

1. *Organic*
   - a. Nitrogenous.
   - b. Non-Nitrogenous.
2. *Inorganic.*

1. Organic.

(*a*) *Nitrogenous bodies* take the chief part in forming the solid tissues of the body, and are found to a considerable extent in the circulating fluids (blood, lymph, chyle), the secretions and excretions. They contain often in addition to Carbon, Hydrogen, Nitrogen, and Oxygen, the elements Sulphur and Phosphorus; but although the composition of most of them is approximately known, no general rational formula can at present be given.

Several classes of animal nitrogenous bodies may be distinguished, and it is convenient to consider them under the following heads:—

(1.) Albuminoids or proteids.
(2.) Gelatinous substances.
(3.) Decomposition nitrogenous bodies.
(4.) Certain supposed nitrogenous bodies, the exact composition of which has not been made out.

(1.) *Albuminoids* or *Proteids* are the most important of the nitrogenous animal compounds, one or more of them entering as essential parts into the formation of all living tissue. In the lymph, chyle, and blood, they also exist abundantly. Their atomic formula is uncertain. Their composition may be taken as—

Carbon	from	51·5	to	54·5	
Hydrogen	,,	6·9	,,	7·3	
Nitrogen	,,	15·2	,,	17·	
Oxygen	,,	20·9	,,	23·5	
Sulphur	,,	·3	,,	2·	(Hoppe-Seyler).

Physical Properties.—Proteids are all amorphous and non-crystallisable, so that they possess as a rule no power (or scarcely any) of passing through animal membranes. They are soluble, but undergo alteration in composition in strong acids and alkalies; some are soluble in water, others in neutral saline solutions, some in dilute acids and alkalies, few in alcohol or ether. Their solutions have a left-handed action on polarised light.

Chemical Properties.—Certain general reactions are given for proteids. They are a little varied in each particular case:—

i.—A solution boiled with strong nitric acid, becomes yellow, and this yellowness gets darker on addition of ammonia (xantho-proteic reaction).

ii.—With potassium ferrocyanide and acetic acid, they give a white precipitate.

iii.—With a trace of copper sulphate and an excess of potassium or sodium hydrate they give a purple coloration.

iv.—With Millon's reagent (mixed nitrate and nitrite of mercury?), they give a white or pinkish precipitate, becoming more pink on boiling.

v.—When boiled with sodium sulphate and acetic acid, a white precipitate is thrown down.

It is usual to place Proteids into the following sub-classes, thus:—

I.	II.	III.
NATIVE ALBUMINS	DERIVED ALBUMINS.	GLOBULIN.
Egg-Albumin.	Acid-Albumin.	(a.) Globulin.
Serum-Albumin.	Alkali-Albumin.	(b.) Myosin.
	Casein.	(c.) Fibrinoplastic Globulin.
		(d.) Fibrinogen.
		(e.) Vitellin, &c.

IV.—FIBRIN. V.—PEPTONES. VI.—COAGULATED PROTEIDS.

VII.—LARDACEIN.

Classes of Proteids.

I. The **Native Albumins** are soluble in water and in saline solutions coagulable by heating, not precipitated by acetic or normal phosphoric acid. Serum-albumin (p. 106) is distinguished from egg-albumin in being soluble in ether and in not so easily giving a precipitate with strong hydrochloric acid; the precipitate being easily redissolved in excess of the acid. Serum-albumin is found in the blood, lymph and serous and synovial fluids, and the tissues generally; it appears in the urine in the condition known as albuminuria. Two varieties, *metalbumin* and *paralbumin* have been described as existing in dropsical fluids and ovarian cysts respectively.

II. **Derived Albumins** are made by adding dilute acids or alkalies to solutions of native-albumin. They are insoluble in water or in neutral saline solutions, and are not coagulated by heat. Both the native-albumins and the next two classes (iii. and iv.) of proteids generally undergo change into either acid- or alkali-albumin on the addition of acids or alkalies, and foods containing either albumins or globulins change first of all into one or other of these compounds, according as they are acted upon by the gastric or pancreatic juices respectively. Acid-albumin is called also *syntonin*, and is either identical with or akin to it. Casein is very probably natural alkali-albumin, and exists in milk, being kept in solution by the alkaline phosphates; it exists also in the serum and serous fluids in small quantity, and in muscle. It is not coagulable by heat, and so corresponds with the other derived albumins; it is obtainable as a precipitate by neutralising milk with acid (acetic). Naturally it is precipitated in sour milk, on the formation of lactic acid.

III. **Globulins** which comprise the fibrin-forming substances of the blood and the coagulable material in muscle, and also the principal part of the crystalline lens, yelk of egg, &c., are soluble in very dilute saline solutions, but not in distilled water like the native-albumins; on addition of an acid or alkali, they are converted into the corresponding derived-albumin. They are precipitated on heating. The following are the chief varieties of globulins.

(a.) *Globulin* or *Crystallin* is prepared by rubbing up the crystalline lens with sand, adding water and filtering. On passing a current of carbonic acid gas through the filtrate, globulin is precipitated. In properties, it resembles fibrinoplastin and fibrinogen, but cannot apparently produce fibrin in fluids containing either. It coagulates at 70°—75° C.

(b.) *Myosin* can be prepared (1) from dead muscle by removing all fat, tendon, &c., and washing repeatedly in water, until the washing contains no trace of proteids, and then treating with 10 per cent. solution of sodium chloride, which will dissolve a large proportion into a viscid fluid, which filters with difficulty. If the viscid filtrate be dropped little by little into a large quantity of distilled water, a white flocculent precipitate of myosin will occur. (2) Or from living muscle by freezing and rubbing up in a mortar with snow and sodium chloride solution 1 per cent., a fluid is obtained which on filtering is at first liquid, but will finally clot, the clot is myosin.

Myosin, on addition of dilute acids, dissolves and forms syntonin or acid-albumin. It is less soluble in dilute saline solutions than (*c*) and (*d*). It coagulates at 55°—60° C.

(c.) *Fibrinoplastin* or *fibrinoplastic globulin* or *paraglobulin* is prepared from blood-serum diluted with 10 vols. of water, by passing a current of carbonic acid gas, and collecting the fine precipitate which is formed, and washing with water containing carbonic acid gas. The current should be strong and not long continued. It may be better prepared as a sticky white substance, by saturating serum with crystallized sodium chloride or magnesium sulphate. (See also p. 85.) It coagulates at 68°—80° C.

(d.) *Fibrinogen* is prepared from hydrocele and other like fluids by diluting and passing a brisk current of carbonic acid gas (CO_2) through the solution; or by saturation of the nerve fluids with sodium chloride or magnesium sulphate. (See also p. 85.) It coagulates at 55°—57° C.

(e.) *Vitellin* can be prepared from yelk of egg, in which it is probably associated with lecithin.

IV. **Fibrin** is a white filamentous body formed in the spontaneous coagulation of certain animal fluids. It is insoluble in water, except at very high temperatures, soluble in dilute acids and alkalies to a slight degree, and in strong neutral saline solutions. Soluble also in strong acids and alkalies.

It is prepared by washing blood-clot or by whipping blood with a bundle of twigs. Its formation in the blood has been already fully considered.

V. **Peptones** (or albuminose) are nitrogenous bodies of uncertain composition made in the process of the digestion of other proteids. It is almost certain that there are several distinct forms.

The great distinction which exists between peptone and other proteids is their diffusibility and they giving no precipitates with either acids or alkalies, with copper sulphate, ferric chloride, potassium ferrocyanide and acetic acid, or on boiling, and only with picric acid, tannin, mercuric chloride, silver nitrate, and lead acetate. In addition to this the colour which a peptone gives with potassium hydrate and cupric sulphate is reddish instead of violet.

Kühne believes that ordinary albumin splits up under the action of the gastric juice or pancreatic juice into two parts, one called *antialbumose*, and the other *hemialbumose*, and further that antialbumose becomes *antipeptone* and hemialbumose, *hemipeptone*. The difference between hemipeptone and antipeptone is that the former can be further split up by the action of the pancreatic juice. He believes that antialbumose is closely allied to syntonin, and that the hemialbumose is more like myosin, and if the pepsin be feebly acting, a body which he calls *antialbumate* appears, which cannot be converted into peptone by gastric juice, but can by pancreatic juice. Solutions of hydrochloric acid or of sulphuric acid, can under favourable circumstances partially change albumin into peptone.

VI.—**Coagulated Proteids**.—When a native albumin, or a globulin is raised to a certain temperature (varying a little with each substance) about 70 C, it undergoes coagulation and loses most of its original characters. It becomes insoluble both in water and in saline solutions, and although soluble in strong acids and alkalies in boiling, partially decomposes during the process. They are not soluble in dilute acids or alkalies, but dissolve freely under the action of the gastric or of the pancreatic secretion, being converted into peptones.

VII. **Lardacein.**—Lardacein or amyloid substance is found in certain organs of the body, chiefly in the liver as a morbid deposit. It is insoluble in water, and in saline solutions. It is unacted upon by the digestive juices. It is coloured red by iodine. It is soluble in acids or in alkalies, thus forming acid- or alkali-albumin.

(2.) *Gelatinous principles* include :—(1.) Gelatin ; (2.) Mucin ; (3.) Elastin ; (4.) Chondrin ; and (5.) Keratin. They are very like the Proteid group, but exhibit considerable differences among themselves.

(1.) *Gelatin* is produced by boiling fibrous tissue, or by treating bones with acids, whereby their salts are dissolved, leaving the framework of gelatin, which is soluble in hot water.

It is a yellow, amorphous, transparent body, which does not give any of the proteid reactions if pure, insoluble in cold, but soluble in hot water, forming a jelly on cooling. Its solutions are precipitated by tannin, by alcohol and by mercuric chloride.

(2.) *Mucin*, contained in mucus. It is a substance of ropy consistency.

Prepared from ox-gall by precipitation with alcohol, and afterwards redissolving in water, and reprecipitating with acetic acid. It may be also prepared from diluting mucus with water, filtering, treating the insoluble portion with weak caustic alkali, and precipitating with acetic acid. It is precipitated by alcohol and mineral acids, but dissolved by excess of the latter—dissolved by alkalies. It gives the proteid reaction with Millon's reagent, but not with cupric sulphate and potassium hydrate. It is not precipitated by mercuric chloride or by tannic acid. It is a colloid substance.

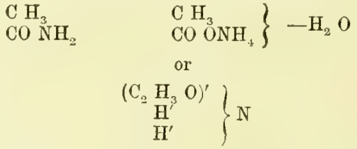
(3.) *Elastin* is the basis of elastic tissue, it is soluble only in strong alkalies on boiling, strong sulphuric or nitric acid dissolves it in the cold.

(4.) *Chondrin* is contained in the matrix of hyaline cartilage, and may be extracted by boiling with water and precipitating with acetic acid.

(5.) *Keratin* is obtained from hair, nails, and dried skin. It contains sulphur evidently only loosely combined.

(3.) *Decomposition Nitrogenous products.*—These are formed by the chemical actions which go on in digestion, secretion, and nutrition.

Most of the compounds are *amides*, which are acids in which *amidogen*, NH_2, is substituted for *hydroxyl*, OH. Amides may also be represented as obtained from the ammonium salts by abstraction of water, or as derived from one or more molecules of ammonia, NH_3, by substituting acid radicals for hydrogen. Thus *acetamide* may be written in any of the following ways :—



$$\begin{array}{l} C\,H_3 \\ CO\,NH_2 \end{array} \qquad \left.\begin{array}{l} C\,H_3 \\ CO\,ONH_4 \end{array}\right\} -H_2\,O$$

or

$$\left.\begin{array}{c} (C_2\,H_3\,O)' \\ H' \\ H' \end{array}\right\} N$$

$(C_2\,H_3\,O)$ being the radical of acetic acid.

Varieties.—Several of the varieties of amides are represented in the products with which we have to do.

(a.) *Monamides* which are derived from a monatomic acid—that is to say, an acid which contains the carboxyl group COOH, once, by the substitution of NH_2 for OH in this group. In these compounds if only one of the H in NH_3 is replaced by an acid radical, a primary monamide is formed ; if two, by acid or alcohol radicals, a secondary monamide ; if three, by acid or alcohol radicals, a tertiary monamide.

Two monamides are also formed from each diatomic acid (*i.e.*, those which contain OH twice, once in the carboxyl group COOH, and once in the alcohol group $C_n\,H_{2n}$ OH), both by the substitution of NH_2 for OH, and therefore having the same composition. They are isomeric and not identical however, the one formed by the substitution of NH_2 for the alcoholic OH being acid, while the other formed by the replacement of the basic hydroxyl is neutral. The acid amides are called *amic acids*, or may form a class by themselves, called *alanines*.

Three amides are obtained from each diatomic and bibasic acid :—(1.) An acid amide or amic acid, derived from the acid ammonium salt by abstraction of one molecule of water. (2.) A neutral monamide (or *imide*), derived by abstraction of two molecules of water from the ammonium salts. (3.) A neutral amide or (b) DIAMIDE, derived from the ammonium salt by abstraction of two molecules of water. Thus succinic acid gives :—

Succinamic Acid	$C_2H_4\left\{\begin{matrix}CO\,NH_2\\CO\,OH\end{matrix}\right.$
Succinimide	$C_2H_4\left\{\begin{matrix}CO\\CO\end{matrix}\right\}NH$
Succinamide	$C_2H_4\ (CO\,NH_2)_2$

(*a*) PRIMARY MONAMIDES.

Glycin, glycocol or glycocin, or amido-acetic acid—$\left.\begin{matrix}(C_2H_3O_2)'\\H'\\H'\end{matrix}\right\}N$ or $\left.\begin{matrix}C_2H_3O\\H_2\end{matrix}\right\}O$ occurs in the body in combination, as in the biliary acids, never free. Glycocholic acid, when treated with weak acids, with alkalies or with baryta water, splits up into cholic acid and glycin, or amido-acetic acid. Thus: $C_{26}H_{43}NO_6 + H_2O = C_{26}H_{40}O_5 + C_2H_5NO_2$. Glycocholic acid + water = cholic acid + glycin, and under similar circumstances Taurocholic acid splits up into cholic acid and taurin:—$C_{26}H_{45}O_3NSO_7 + H_2O = C_{26}H_{40}O_5 + C_2H_7NSO_3$, or amido-isethionic. Taurocholic acid + water = cholic acid and taurin. Glycin occurs also in hippuric acid. It can be prepared from gelatin by the action of acids or alkalies, it can also be obtained from hippuric acid.

Leucin.—or amido-caproic acid, $\left.\begin{matrix}C_6H_{11}O_2\\H\\H\end{matrix}\right\}ON$, or $\left.\begin{matrix}C_6H_{11}O\\NH_2\end{matrix}\right\}O$ occurs normally in many of the organs of the body and is a product of the pancreatic digestion of proteids. It is present in the urine in certain diseases of the liver in which there is loss of substance, especially in acute yellow atrophy. It occurs in circular oily discs or crystallises in plates, and can be prepared either by boiling horn shavings, or any of the gelatins, with sulphuric acid, or out of the products of pancreatic digestion.

Sarcosin may be considered as methyl glycin, $\left.\begin{matrix}C_2H_3O_2\\CH_3\\H\end{matrix}\right\}N$. It is a constituent of kreatin, but has never been found free in the human body.

Neurin ($C_5H_{13}NO$), is an unstable body, which has been found in ox and pig's gall.

Taurin, $C_2H_7NSO_3$ or $\left.\begin{matrix}C_2H_5\\SO_2HO\\H\end{matrix}\right\}N$; or amido-isethionic acid, is a constituent of the bile acid, taurocholic acid, and is found also in traces in the muscles and lungs.—See above.

Cystin, $C_3H_7NSO_2$ occurs in a rare form of urinary calculus, which is only formed in a urine of neutral reaction. It can be crystallised in hexagonal laminæ of pale yellow colour, becoming greenish on exposure to light.

Hippuric Acid. $C_9H_9NO_3$, or $\left.\begin{matrix}C_2H_3O_2\\C_7H_5O\\H\end{matrix}\right\}N$, or benzolglycin, a normal constituent of human urine, the quantity excreted being increased by a vegetable diet, and therefore it is present in greater amount in the urine of herbivora. It may be decomposed by acids into glycin and benzoic acid. It crystallises in semi-transparent rhombic prisms, almost insoluble in cold water, soluble in boiling water. (See also p. 446).

Tyrosin, $C_9 H_{11} NO_3$, is found, generally together with leucin, in certain glands, *e.g.* pancreas and spleen; and chiefly in the products of pancreatic digestion or of the putrefaction of proteids. It is found in the urine in some diseases of the liver, especially acute yellow atrophy. It crystallises in fine needles, which collect into feathery masses. It gives the proteid test with Millon's reagent, and heated with strong sulphuric acid, on the addition of ferric chloride gives a violet colour.

Lecithin, $C_{42} H_{84} P NO_9$, is a phosphoretted fatty body, which has been found mixed with cerebrin, and oleophosphoric acid in the brain. It is also found in blood, bile and serous fluids, and in larger quantities in nerves, pus, yelk of egg, semen, and white blood-corpuscles. On boiling with acids it yields cholin, glycero-phosphoric acid, palmic and oleic acids.

Cerebrin, $C_{17} H_{33} NO_3$, is found in nerves, pus-corpuscles, and in the brain. Its chemical constitution is not known. It is a light amorphous powder, tasteless and odourless. Swells up like starch when boiled with water, and is converted by acids into a saccharine substance and other bodies. The so-called *Protagon* is a mixture of lecithin and cerebrin.

(*b.*) PRIMARY DIAMIDES OR UREAS.

Urea, $(NH_2)_2 CO$, is the last product of the oxidation of the albuminous tissues of the body and of the albuminous foods. It occurs as the chief nitrogenous constituent of the urine of man, and of some other animals. It has been found in the blood and serous fluids, lymph, and in the liver.

Properties. Crystallises in thin glittering needles, or in prisms with pyramidal ends. Easily soluble in water and alcohol, insoluble in ether, easily decomposed by strong acids, readily forms compounds with acids and bases, of which the chief are $(NH_2)_2 COHNO_3$, *urea nitrate*, and $((N H_2)_2 CO)_2 H_2 C_2 O_2 + H_2 O$, *urea oxalate*.

Constitution.—It is usually considered to be a diamide of carbonic acid which may be written $\begin{matrix}CO\\H_2\\H_2\end{matrix} N_2$, or $CO \left.\begin{matrix}N H_2\\N H_2\end{matrix}\right\}$ which is $CO (HO)_2$, with $(OH)'_2$, replaced by $(NH_2)'_2$. Some think it a monamide of carbamic acid, CO, OH, NH_2, thus $CO, NH_2\ NH_2$, with one atom of NH_2, or amidogen in place of one of hydroxyl OH.

Urea is isomeric with ammonium cyanate $C \left\}\begin{matrix}N\\ONH_4\end{matrix}\right.$ from which it was first artificially prepared.[1]

Kreatin, $C_4 H_9 N_3 O_2$, is one of the primary products of muscular disintegration. It is always found in the juice of muscle. It is generally decomposed in the blood into urea and kreatinin, and seldom, unless under abnormal circumstances, appears as such in the urine. Treated with either sulphuric or hydrochloric acid, it is converted into kreatinin ; thus—

$$C_4 H_9 N_3 O_2 = C_4 H_7 N_3 O + H_2 O.$$

Kreatinin, $C_4 H_7 N_3 O$, is present in human urine, derived from oxidation of kreatin. It does not appear to be present in muscle.

(*c.*) UREIDES.

Ureides are a third variety of amides, and may be considered as ureas in which part of the hydrogen is replaced by diatomic acid radicals. *Monoureides* contain one acid radical and one urea residue; and *diureides*, one acid radical and two urea residues.

Uric Acid, $C H_4 N_4 O_3$, occurs in the urine, sparingly in human urine, abundantly in that of birds and reptiles, where it represents the chief nitrogenous decomposition product. It occurs also in the blood, spleen, liver, and sometimes is the only constituent of urinary calculi. It is probably converted in the blood into urea and some carbon acid. It generally occurs in urine in combination with bases, forming *urates*, and never free unless under abnormal conditions. A deposit of urates may occur when the urine is concentrated or extremely acid, or when, as during febrile disorders, the conversion of uric acid into urea is incompletely performed.

Properties.—Crystallises in many forms, of which the most common are smooth, transparent, rhomboid plates, diamond-shaped plates, hexagonal tables, &c. Very insoluble in water, and absolutely so in alcohol and ether. Dried with strong nitric acid in a water bath, a compound is formed called *alloxan*, which gives a beautiful violet red with ammonium hydrate (*murexide*), and a blue colour with potassium hydrate. It is easily precipitated from its solutions by the addition of a free acid. It forms both acid and neutral salts with bases. The most soluble urate is lithium urate.

Composition.—Very uncertain; has been however recently produced artificially, but it is not easily decomposed; it may be regarded as diureide of tartronic acid. The chief product of its decomposition is urea.

Guanin, $C_5 H_5 N_5 O$, has been found in the human liver, spleen, and fæces, but does not occur as a constant product.

Xanthin, $C_5 H_4 N_4 O_2$, has been obtained from the liver, spleen, thymus, muscle, and the blood. It is found in normal urine, and is a constituent of certain rare urinary calculi.

Hypoxanthin, $C_5 H_4 N_4 O$, *or sarkin*, is found in juice of flesh, in the spleen, thymus, and thyroid.

Allantoin, $C_4 H_6 N_4 O_3$, found in the allantoic fluid of the fœtus, and in the urine of animals for a short period after their birth. It is one of the oxidation products of uric acid, which on oxidation gives urea.

In addition to the amides and probably related to them, are certain colouring and excrementitious matters, which are also most likely distinct decomposition compounds.

Pigments, &c.

Bilirubin, $C_9 H_9 NO_2$, is the best known of the bile pigments. It is best made by extracting inspissated bile or gall stones with water (which dissolves the salts,

&c.), then with alcohol, which takes out cholesterin, fatty, and biliary acids. Hydrochloric acid is then added, which decomposes the lime salt of bilirubin and removes the lime. After extracting with alcohol and ether, the residue is dried and finally extracted with chloroform. It crystallizes of a bluish-red colour. It is allied in composition to hæmatin.

Biliverdin, $C_8 H_9 NO_2$, is made by passing a current of air through an alkaline solution of bilirubin, and by precipitation with hydrochloric acid. It is a green pigment.

Bilifuscin, $C_9 H_{11} NO_3$, is made by treating gall stones with ether, then with dilute acid, and extracting with absolute alcohol. It is a non-crystallizable brown pigment.

Biliprasin is a pigment of a green colour, which can be obtained from gall stones.

Bilihumin (Staedeler) is a dark brown earthy-looking substance, of which the formula is unknown.

Urobilin occurs in bile and in urine, and is probably identical with *stercobilin*, which is found in the fæces.

Uroerythrin is one of the colouring matters of the urine. It is orange red, and contains iron.

Melanin is a dark brown or black material containing iron, occurring in the lungs, bronchial glands, the skin, hair, and choroid.

Hæmatin has been fully treated of in Chapter IV.

Indican is supposed to exist in the sweat and urine. It has not however been satisfactorily isolated.

Indigo, $C_8 H_5 N_9 O$, is formed from indican, and gives rise to the bluish colour which is occasionally met with in the sweat and urine.

Indol, $C_8 H_2 N$, is found in the fæces, and is formed either by decomposition of indigo, or of the proteid food materials. It gives the characteristic disagreeable smell to fæces.

(4.) *Nitrogenous Bodies of Uncertain Nature.*

Ferments are bodies which possess the property of exciting chemical changes in matter with which they come in contact. They are at present divided into two classes, called (1) organised, and (2) unorganised or soluble. (1,) Of the *organised*, yeast may be taken as an example. Its activity depends upon the vitality of the yeast cell, and disappears as soon as the cell dies, neither can any substance be obtained from the yeast by means of precipitation with alcohol or in any other way which has the power of exciting the ordinary change produced by yeast.

(2.) *Unorganised or soluble ferments* are those which are found in secretions of glands, or are produced by chemical changes in animal or vegetable cells in general; when isolated they are colourless, tasteless, amorphous solids soluble in water and glycerin, and precipitated from the aqueous solutions by alcohol and acetate of lead. Chemically many of these are said to contain nitrogen.

Mode of action.—Without going into the theories of how these unorganised ferments act, it will suffice to mention that:

(1.) Their activity does not depend upon the actual amount of the ferment present. (2.) That the activity is destroyed by high temperature, and various concentrated chemical reagents, but increased by moderate heat, about 40° C., and by weak solutions of either an acid or an alkaline fluid. (3.) The ferments themselves appear to undergo no change in their own composition, and waste very slightly during the process.

Varieties.—The chief classes of unorganised ferments are :—

(1.) *Amylolytic*, which possess the property of converting starch into glucose. They add a molecule of water, and may be called hydrolytic. The probable reaction is as follows :

$$\underset{\text{Starch}}{3\ C_6\ H_{10}\ O_3} + \underset{\text{Water}}{3\ H_{20}} = \underset{\text{Glucose}}{C_6\ H_{12}\ O_6} + \underset{\text{Dextrin}}{2\ C_6\ H_{10}\ O_5} = \underset{\text{Glucose.}}{3\ C_6\ H_{12}\ O_6}$$

This shows that there is an intermediate reaction, the starch being first turned only partly into glucose and principally into dextrin, which is afterwards further converted into glucose. The principal amylolytic ferments are *Ptyalin*, found in the saliva, and a ferment, probably distinct in the pancreatic juice called *Amylopsin.* These both act in an alkaline medium. Amylolytic ferments have been found in the blood and elsewhere.

Conversion of starch into sugar.—With reference to the action of the amylolytic ferments, recent observations have shown that the starch molecule is not by any means so simple as it has been represented above. As it is said that starchy materials, in the form of wheat and other cereals, and in the potato or its substitutes, form two-thirds of the total food of man, it is very important that we should note (1) the changes which occur in starch on cooking, and (2) the series of reactions it undergoes during its conversion by the amylolytic ferments into sugar.

(1.) The object of this change is to produce gelatinous or soluble starch. A starch granule consists of two parts : an envelope of *cellulose*, which gives a blue colour with iodine on addition of sulphuric acid, and of *granulose*, which is contained within it, giving a blue with iodine alone. Brücke states that a third body is contained in the granule, which gives a red with iodine, viz., *erythro-granulose.* On boiling, the granulose swells up, bursts the envelope, and the whole granule is more or less completely converted into a paste or into mucilaginous gruel.

(2.) Changes which occur on addition of an amylolytic ferment. On the addition of saliva or extract of pancreas to gelatinous starch, the first change noticed is that the paste liquifies very quickly, but the liquid does not give the reaction for dextrin or for sugar ; but soon this latter reaction appears, increasing very considerably and quickly, although at first, in addition, a reaction of erythrodextrin, a red on addition of iodine, is found ; as the sugar increases, however, this disappears. At first the erythrodextrin is mixed with starch, as the reaction is a reddish purple with iodine, then it is a pure red, and finally a yellowish brown. As the sugar continues to increase the reaction with iodine disappears, but it is said that dextrin is still present in the form of achroo-dextrines, which give no reaction with iodine. However long the reaction goes on, it is unlikely that all the dextrin becomes sugar.

Next with regard to the kind of sugar formed, it is, at first at any rate, not *glucose* but *maltose*, the formula for which is $C_{12}\ H_{22}\ O_{11}$. Maltose is allied to saccharose or cane sugar more nearly than to glucose ; it is crystalline ; its solution has the property of polarising light to a greater degree than solutions of glucose ; is not so sweet, and reduces copper sulphate less easily. It can be converted into glucose by boiling with dilute acids.

According to Brown and Heron the reactions may be represented thus :—

One molecule of gelatinous starch is converted into *n* molecules of soluble starch.

One molecule of soluble starch = 10 ($C_{12}H_{20}O_{10}$) + 8 (H_2O)
= 1 Erythro-dextrin (giving red with iodine) Maltose.
9 ($C_{12}H_{20}O_{10}$) + ($C_{12}H_{22}O_{11}$)
= 2. Erythro-dextrin (giving yellow with iodine) Maltose.
8 ($C_{12}H_{20}O_{10}$) + 2 ($C_{12}H_{22}O_{11}$)
= 3. Achroo-dextrin Maltose.
7 ($C_{12}H_{20}O_{10}$) + 3 ($C_{12}H_{22}O_{11}$)

And so on; the resultant being:—

$$\underset{\text{Soluble starch}}{10\,(C_{12}H_{20}O_{10})} + \underset{\text{Water}}{8\,(H_2O)} = \underset{\text{Maltose}}{8\,(C_{12}H_{22}O_{11})} + \underset{\text{Achroo-dextrin.}}{2\,(C_{12}H_{20}O_{10})}$$

Pancreatic juice and intestinal juice are able to turn the achroo-dextrin which remains into maltose, and maltose into glucose (dextrose). It is doubtful whether saliva possesses the same power.

(2.) *Proteolytic* convert proteids into peptones. The nature of their action is probably hydrolytic. The proteolytic ferments of the body are called *Pepsin*, acting in an acid medium from the gastric juice. *Trypsin*, acting in an alkaline medium from the pancreatic juice. The Succus entericus is said to contain a third such ferment.

(3.) *Inversive*, which convert cane sugar or *saccharose* into grape sugar or *glucose*. Such a ferment was found by Claude Bernard in the Succus entericus; and probably exists also in the stomach mucus.

$$\underset{\text{Saccharose}}{2\,C_{12}H_{22}O_{11}} + \underset{\text{Water}}{2\,H_2O} = \underset{\text{Dextrose}}{C_{12}H_{24}O_{12}} + \underset{\text{Lævulose}}{C_{12}H_{24}O_{12}}$$

(4.) *Ferments which act upon fats*, such a body called *Steapsin*, has been found in pancreatic juice.

The ferments *Amylopsin*, *Trypsin*, and *Steapsin*, are said to exist separately in pancreatic juice, and if so, make up what was formerly called *Pancreatin*, and which was said to have the functions of the three.

(5.) *Milk-curdling ferments.* It has been long known that rennet, a decoction of the fourth stomach of a calf, in brine, possessed the power of curdling milk. This power does not depend upon the acidity of the gastric juice, since the curdling will take place in a neutral or alkaline medium; neither does it depend upon the *pepsin*, as pure pepsin scarcely curdles milk at all, and the rennet which rapidly curdles milk has a very feeble proteolytic action. From this and other evidence it is believed that a distinct milk-curdling ferment exists in the stomach. W. Roberts has shown that a similar but distinct ferment exists in pancreatic extract, which acts best in an alkaline medium, next best in an acid medium, and worst in a neutral medium. The ferment of rennet acts best in an acid medium, and worst in an alkaline, the reaction ceasing if the alkalinity be more than slight.

In addition to the above ferments, many others most likely exist in the body, of which the following are the most important:

6. Fibrin-forming ferment (Schmidt), (see p. 85, *et seq.*), found in the blood, lymph and chyle.

7. A ferment which converts glycogen into glucose in the liver; being therefore an amylolytic ferment.

8. Urinary ferments.

(*b.*) *Organic non-nitrogenous bodies* consist of—(1.) Oils and fats. (2.) Amyloids. (3.) Acids.

(1.) OILS AND FATS.

Saponifiable.		*Non-saponifiable.*	
Palmitin	$C_{51}H_{90}O_6$	Cholesterin	$C_{20}H_{44}O$
Stearin	$C_{57}H_{110}O_6$	Stercorin	?
Olein	$C_{57}H_{104}O_6$	Excretin	$C_{78}H_{150}SO_2$

Constitution.

The Saponifiable fats are formed by the union of fatty acid radicals with the triatomic alcohol, *Glycerin* $C_3H_5(OH)_3$. The radicals are $C_{18}H_{35}O$, $C_{16}H_{31}O$, and $C_{18}H_{33}O$, respectively. Human fat consists of a mixture of *palmitin*, *stearin*, and *olein*, of which the two former contribute three-quarters of the whole. Olein is the only liquid constituent.

General characteristics.—Insoluble in water and in cold alcohol; soluble in hot alcohol, ether, and chloroform. Colourless and tasteless; easily decomposed or saponified by alkalies or super-heated steam into glycerin and the fatty acids.

Non-Saponifiable.—*Cholesterin*, $C_{26}H_{44}O$, is the only alcohol which has been found in the body in a free state. It occurs in small quantities in the blood and various tissues, and forms the principal constituent of gall-stones. It is found in dropsical fluids, especially in the contents of cysts, in disorganised eyes, and in plants (especially peas and beans). It is soluble in ether, chloroform, or benzol. It crystallises in white feathery needles. See also under the head of the constituents of the bile.

Excretin (Marcet), and *Stercorin* (Flint), are crystalline fatty bodies which have been isolated from the fæces.

(2.) AMYLOIDS.

Amyloids.—Under this head are included both starch and sugar. The substances, like the fats, contain carbon, hydrogen, and oxygen; but the last-named element is present in much larger relative amount, the hydrogen and oxygen being in the proportion to form water.

The following varieties of these substances are found in health in the body.

(*a*) *Glycogen* ($C_6H_{10}O_5$).—This substance, which is identical in composition with starch, and like it, is readily converted into sugar by ferments, is found in many embryonic tissues and in all new formations where active cell-growth is proceeding. It is present also in the placenta. After birth it is found almost exclusively in the liver and muscles.

Glycogen is formed chiefly from the saccharine matters of the food; but although its amount is much increased when the diet largely consists of starch and sugar, these are not its only source. It is still formed when the diet is flesh only, by the decomposition, probably, of albumin into glycogen and urea.

The destination of glycogen has been considered in a former chapter. (See p. 350.)

(*b*) *Glucose* or *grape-sugar* ($C_6 H_{12} O_6 + H_2 O$) is found in minute quantities in the blood and liver, and occasionally in other parts of the body. It is derived directly from the starches and sugars in the food, or from the glycogen which has been formed in the body from these or other matters. However formed, it is in health quickly burnt off in the blood by union with oxygen, and thus helps in the maintenance of the body's temperature. Like other amyloids it is one source whence fat is derived.

(*c*) *Lactose* or *sugar of milk* ($C_{12} H_{22} O_{11} + H_2 O$), is formed in large quantity when the mammary glands are in a condition of physiological activity,—human milk containing 5 or 6 per cent. of it. Like other sugars it is a valuable nutritive material, and hence is only discharged from the body when required for the maintenance of the offspring. The same remark is applicable to the other organic nutrient constituents of the milk, albumin and saponifiable fats, which, if we except what is present in the secretions of the generative organs, are discharged from the body only under the same conditions and in the same secretion.

(*d*) *Inosite* ($C_6 H_{12} O_6 + 2 H_2 O$), a variety of sugar, identical in composition with glucose, but differing in some of its properties, is found constantly in small amount in muscle, and occasionally in other tissues. Its origin and uses, in the economy are, presumably, similar to those of glycogen.

(*e*) *Maltose* ($C_{12} H_{22} O_{11}$), is formed in the conversion of starch into glucose (see p. 853).

(3) ORGANIC ACIDS.

GROUP I.—MONATOMIC FATTY ACIDS.

Formic	$C\ HO\ OH$	Caproic	$C_6 H_{11} O\ OH$
Acetic	$C_2 H_3 O\ OH$	Capric	$C_8 H_{15} O\ OH$
Propionic	$C_3 H_5 O\ OH$	Palmitic	$C_{16} H_{31} O\ OH$
Butyric	$C_4 H_7 O\ OH$	Stearic	$C_{18} H_{35} O\ OH$
Valerianic	$C_5 H_9 O\ OH$	Oleic	$C_{18} H_{33} O\ OH$

Formic, acetic, and propionic acids are present in sweat, but normally in no other human secretion. They have been found elsewhere in diseased conditions. Butyric acid is found in sweat. Various others of these acids have been obtained from blood, muscular juice, fæces, and urine.

GROUP II.—DIATOMIC FATTY ACIDS.

Monobasic.		*Bibasic.*	
Glycolic	$C_2 H_4 O_3$	Oxalic	$C_2 H_2 O_4$
Lactic	$C_3 H_6 O_3$	Succinic	$C_4 H_6 O_4$
Leucic	$C_6 H_{12} O_3$	Sebacic	$C_{10} H_{10} O_4$

Lactic acid exists in a free state in muscular plasma, and is increased in quantity by muscular contraction, is never contained in healthy blood, and when present in abnormal amount seems to produce rheumatism.

Oxalates are present in the urine in certain diseases, and after drinking certain carbonated beverages, and after eating rhubarb, &c.

AROMATIC SERIES.

Benzoic	$C_7 H_6 O_2$
Phenol	$C_6 H_6 O$

Benzoic acid is always found in the urine of herbivora, and can be obtained from stale human urine. It does not exist free elsewhere.

Phenol.—Phenyl alcohol or *carbolic acid* exists in minute quantity in human urine. It is an alcohol of the aromatic series.

2. Inorganic Principles.

The inorganic proximate principles of the human body are numerous. They are derived, for the most part, directly from food and drink, and pass through the system unaltered. Some are, however, decomposed on their way, as chloride of sodium, of which only four-fifths of the quantity ingested are excreted in the same form ; and some are newly formed within the body,—as for example, a part of the sulphates and carbonates, and some of the water.

Much of the inorganic saline matter found in the body is a necessary constituent of its structure,—as necessary in its way as albumin or any other organic principle ; another part is important in regulating or modifying various physical processes, as absorption, solution, and the like ; while a part must be reckoned only as matter, which is, so to speak, accidentally present, whether derived from the food or the tissues, and which will, at the first opportunity, be excreted from the body.

Gases.—The gaseous matters found in the body are *Oxygen*, *Hydrogen*, *Nitrogen*, *Carburetted* and *Sulphuretted hydrogen*, and *Carbonic acid*. The first three have been referred to (p. 843). Carburetted and sulphuretted hydrogen are found in the intestinal canal. Carbonic acid is present in the blood and other fluids, and is excreted in large quantities by the lungs, and in very minute amount by the skin. It will be specially considered in the chapter on Respiration.

Water, the most abundant of the proximate principles, forms a large proportion,—more than two-thirds of the weight of the whole body. Its relative amount in some of the principal solids and fluids of the body is shown in the following table (quoted by Dalton, from Robin and Verdeil's table, compiled from various authors) :—

Quantity of Water in 1000 Parts.

Teeth	100	Bile	880
Bones	130	Milk	887
Cartilage	550	Pancreatic juice	900
Muscles	750	Urine	936
Ligament	768	Lymph	960
Brain	789	Gastric juice	975
Blood	795	Perspiration	986
Synovia	805	Saliva	995

Uses of the Water of the Body.—The importance of water as a constituent of the animal body may be assumed from the preceding table, and is shown in a still more striking manner by its withdrawal. If any tissue,—as muscle, cartilage, or tendon be subjected to heat sufficient to drive off the greater part of its water, all its characteristic physical properties are destroyed ; and what was previously soft, elastic, and flexible, becomes hard and brittle, and horny, so as to be scarcely recognisable.

In all the fluids of the body—blood, lymph, &c., water acts the part of a general solvent, and by its means alone circulation of nutrient matter is possible. It is the medium also in which all fluid and solid aliments are dissolved before absorption, as well as the means by which all, except gaseous, excretory products are removed. All the various processes of secretion, transudation, and nutrition, depend of necessity on its presence for their performance.

Source.—The greater part, by far, of the water present in the body is taken into it as such from without, in the food and drink. A small amount, however, is the result of the chemical union of hydrogen with oxygen in the blood and tissues. The total amount taken into the body every day is about $4\frac{1}{2}$ lbs. ; while an uncertainty quantity (perhaps $\frac{1}{2}$ to $\frac{3}{4}$ lb.) is formed by chemical action within it.—(Dalton.)

Loss.—The loss of water from the body is intimately connected with excretion from the lungs, skin, and kidneys, and, to a less extent, from the alimentary canal. The loss from these various organs may be thus apportioned (quoted by Dalton from various observers).

From the Alimentary Canal (fæces)	4 per cent.
,, Lungs	20 ,,
,, Skin (perspiration)	30 ,,
Kidneys (urine)	46 ,,
	100

Sodium and Potassium Chlorides are present in nearly all parts of the body. The former seems to be especially necessary, judging from the instinctive craving for it on the part of animals in whose food it is deficient, and from the diseased condition which is consequent on its withdrawal. In the blood, the quantity of chloride of sodium is greater than that of all its other saline ingredients taken together. In the muscles, on the other hand, the quantity of chloride of sodium is less than that of the chloride of potassium.

Calcium Fluoride, in minute amount, is present in the bones and teeth, and traces have been found in the blood and some other fluids.

Calcium, Potassium, Sodium, and Magnesium Phosphates are found in nearly every tissue and fluid. In some tissues—the bones and teeth—the phosphate of calcium exists in very large amount, and is the principal source of that hardness of texture, on which the proper performance of their functions so much depends. The phosphate of calcium is intimately incorporated with the organic basis or matrix, but it can be removed by acids without destroying the general shape of the bone ; and, after the removal of its inorganic salts, a bone is left soft, tough, and flexible.

Potassium and sodium phosphates with the carbonates, maintain the alkalinity of the blood.

Calcium Carbonate occurs in bones and teeth, but in much smaller quantity than the phosphate. It is found also in some other parts. The small concretions of the internal ear (otoliths) are composed of crystalline carbonate of calcium, and form the only example of inorganic crystalline matter existing as such in the body.

Potassium and Sodium Carbonates are found in the blood, and some other fluids and tissues.

Potassium, Sodium, and Calcium Sulphates are met with in small amount in most of the solids and fluids.

Silicon.—A very minute quantity of *silica* exists in the urine, and in the blood. Traces of it have been found also in bones, hair, and some other parts.

Iron.—The especial place of *iron* is in hæmoglobin, the colouring-matter of the blood, of which a further account has been given with the chemistry of the blood. Peroxide of iron is found, in very small quantities, in the ashes of bones, muscles, and many tissues, and in lymph and chyle, albumin of serum, fibrin, bile, and other fluids ;

and a salt of iron, probably a phosphate, exists in the hair, black pigment, and other deeply coloured epithelial or horny substances.

Aluminium, Manganese, Copper, and Lead.—It seem, most likely that in the human body, *copper*, *manganesium*, *aluminium* and *lead* are merely accidental elements, which, being taken in minute quantities with the food, and not excreted at once with the fæces, are absorbed and deposited in some tissue or organ, of which, however, they form no necessary part. In the same manner, *arsenic*, being absorbed, may be deposited in the liver and other parts.

APPENDIX B.

MEASURES OF WEIGHT (*Avoirdupois*).

(*Averages.*)

	lbs.	ozs.
Recent Skeleton	21	8
Muscles and Tendons	77	8
Skin and Subcutaneous tissue	16	5
Blood	11 to 14	–
Brain Cerebrum	2	12
Cerebellum	–	5¼
Pons and Medulla oblongata	–	1
Encephalon	3	2¼
Eyes	–	½
Heart	–	10
Intestines, small	1	11½
„ large	1	1
Kidneys (both)	–	10½
Larynx, Trachea, and larger Bronchi	–	

	lbs.	ozs.
Liver	3	8
Lungs (both)	2	10
Œsophagus	–	1¾
Ovaries (both) ¼ to	–	½
Pancreas	–	3
Salivary Glands (both sides), 1½ to	–	2
Stomach	–	7
Spinal Cord, divested of its nerves and membranes	–	1½
Spleen	–	7
Suprarenal Capsules (both), ⅛ to	–	¼
Testicles (both) 1½ to	–	2
Thyroid body and remains of Thymus gland	–	¾
Tongue and Hyoid bone	–	3
Uterus (virgin) ½ to	–	¾

MEASURES OF LENGTH (*Average*).

	ft.	in.
Appendix vermiformis 3 to	–	6
Bronchus, right	–	1½
„ left	–	2½
Cæcum	–	2½
Duct, common bile	–	3
„ „ ejaculatory, ¾ to	–	1
„ of Cowper's gland	–	1¼
„ hepatic	–	2
„ nasal	–	–¾
„ parotid	–	2½
„ sub-maxillary	–	2¾
Epididymis	–	1¾
„ unravelled	20	–
Eustachian tube	–	1½
Fallopian tube	–	3½
Intestine, large	5 to 6	–
„ small	20	–
Ligament, round, of uterus	–	4½

	ft.	in.
Ligament of ovary	–	1½
Meatus auditorius externus	–	1¼
Medulla oblongata	–	1¼
Œsophagus	–	10
Pancreas	–	7
Pharynx	–	4½
Rectum	–	8
Spinal cord	1	5
Tubulus seminiferus	2	3
Urethra, male	–	8
„ female	–	1½
Ureter	1	4
Vagina 4 to	–	6
Vas deferens	2	–
Vesicula seminalis	–	2
„ „ unravelled, 4 to	–	6
Vocal cord	–	–½

SIZES OF VARIOUS HISTOLOGICAL ELEMENTS AND TISSUES.

Average size in fractions of an inch.

Air-cells, $\frac{1}{70}$ to $\frac{1}{50}$.
Blood-cells (red), $\frac{1}{3200}$ (breadth).
,, ,, $\frac{1}{10000}$ (thickness).
,, (colourless), $\frac{1}{2500}$.
Canaliculus of bone, $\frac{1}{7000}$ (width).
Capillary blood-vessels, $\frac{1}{3000}$ (lung) to $\frac{1}{1200}$ (bone).
Cartilage-cells (nuclei of), $\frac{1}{3000}$.
Chyle-molecules, $\frac{1}{30000}$.
Cilia, $\frac{1}{5000}$ to $\frac{1}{2500}$ (length).
Cones of retina (at yellow spot), $\frac{1}{12000}$ to $\frac{1}{10000}$ (width).
Connective-tissue fibrils, $\frac{1}{50000}$ to $\frac{1}{15000}$ (width).
Dentine-tubules, $\frac{1}{4500}$ (width).
Enamel-fibres, $\frac{1}{5000}$ (width).
End-bulbs, $\frac{1}{600}$.
Epithelium
columnar (intestine), $\frac{1}{2000}$ (length).
spheroidal (hepatic), $\frac{1}{1000}$ to $\frac{1}{800}$.
squamous (peritoneum) $\frac{1}{10000}$ (width).
,, (mouth), $\frac{1}{600}$,,
,, (skin), $\frac{1}{800}$,,
Elastic (yel.) fibres, $\frac{1}{24000}$ to $\frac{1}{4000}$ (wide).
Fat-cells, $\frac{1}{500}$ to $\frac{1}{400}$.
Germinal vesicle, $\frac{1}{720}$.
,, spot, $\frac{1}{3000}$.
Glands
gastric, $\frac{1}{60}$ to $\frac{1}{20}$ (length).
,, $\frac{1}{500}$ to $\frac{1}{300}$ (width).
Lieberkuhn's (small intestines), $\frac{1}{350}$ to $\frac{1}{250}$ (length).
Lieberkuhn's (small intestine), $\frac{1}{600}$ (width).
Peyer's (follicles), $\frac{1}{24}$ to $\frac{1}{12}$.
Sweat, $\frac{1}{70}$ (width).
,, in axilla, $\frac{1}{30}$ to $\frac{1}{8}$ (width).
Haversian canals, $\frac{1}{1000}$ to $\frac{1}{200}$ (width).
Lacunæ (bone), $\frac{1}{1800}$ (length).
,, ,, $\frac{1}{3000}$ (width).
Macula lutea, $\frac{1}{24}$.
Malpighian bodies (kidney), $\frac{1}{120}$.
,, corpuscles (spleen), $\frac{1}{60}$ to $\frac{1}{30}$.
Muscle (striated), $\frac{1}{500}$ to $\frac{1}{400}$ (width).
,, -cell (plain), $\frac{1}{600}$ to $\frac{1}{300}$ (length).
,, ,, ,, $\frac{1}{4500}$ to $\frac{1}{3500}$ (width).
Nerve-corpuscles (brain), $\frac{1}{3000}$ to $\frac{1}{300}$.
,, -fibres (medullated) $\frac{1}{12000}$ to $\frac{1}{1500}$ (width).
(non-medullated) $\frac{1}{8000}$ to $\frac{1}{5000}$ (width).
Ovum, $\frac{1}{120}$.
Pacinian bodies, $\frac{1}{15}$ to $\frac{1}{10}$. (length).
,, ,, $\frac{1}{25}$ to $\frac{1}{20}$. (width).
Papillæ of skin (palm), $\frac{1}{200}$ to $\frac{1}{100}$ (length).
,, ,, (face), $\frac{1}{800}$ to $\frac{1}{500}$,,
,, tongue (circumvallate), $\frac{1}{20}$ to $\frac{1}{12}$ (width).
,, ,, (fungiform), $\frac{1}{35}$ to $\frac{1}{25}$ (width).
,, ,, (filiform), $\frac{1}{10}$ (length).
Pigment-cells of choroid (hexagonal), $\frac{1}{1000}$.
,, granules, $\frac{1}{20000}$.
Spermatozoon, $\frac{1}{600}$ to $\frac{1}{500}$ (length).
,, head, $\frac{1}{5000}$,,
,, ,, $\frac{1}{10000}$ (width).
Touch-corpuscle, $\frac{1}{300}$ (length).
Tubuli seminiferi, $\frac{1}{200}$ to $\frac{1}{100}$ (width).
,, uriniferi, $\frac{1}{600}$.
Villi, $\frac{1}{50}$ to $\frac{1}{8}$ (length).
,, $\frac{1}{250}$ to $\frac{1}{70}$ (width).

SPECIFIC GRAVITY OF VARIOUS FLUIDS AND TISSUES.

(*Water* = 1·000.)

Adipose tissue	0·932
Bile	1·020
Blood	1·055
„ corpuscles (red)	1·088
Body (entire)	1·065
Bone	1·870 to 1·970
Brain	1·036
„ grey matter	1·034
„ white	1·040
Cartilage	1·150
Cerebro-spinal fluid	1·006
Chyle	1·024
Gastric juice	1·0023
Intestinal juice	1·011
Kidney	1·052
Liquor amnii	1·008
Liver	1·055
Lymph	1·020
Lungs	
when fully distended	0·126
ordinary condition, post mortem	0·345 to 0·746
when deprived of air	1·056
Muscle	1·020
Milk	1·030
Pancreatic juice	1·012
Saliva	1·006
Serum	1·026
Spleen	1·060
Sweat	1.004
Urine	1·020

TABLE SHOWING THE PERCENTAGE COMPOSITION OF VARIOUS ARTICLES OF FOOD. (LETHEBY.)

	Water.	Albumin.	Starch.	Sugar.	Fat.	Salts.
Bread	37	8·1	47·4	3·6	1·6	2·3
Oatmeal	15	12·6	58·4	5·4	5·6	3·
Indian corn meal	14	11·1	64·7	0·4	8·1	1·7
Rice	13	6·3	79·1	0·4	0·7	0·5
Arrowroot	18	—	82·	—	—	—
Potatoes	75	2·1	18·8	3·2	0·2	0·7
Carrots	83	1·3	8·4	6·1	0·2	1·0
Turnips	91	1·2	5·1	2·1	—	0·6
Sugar	5	—	—	95·0	—	—
Treacle	23	—	—	77·0	—	—
Milk	86	4·1	—	5·2	3·9	0·8
Cream	66	2·7	—	2·8	26·7	1·8
Cheddar cheese	36	28·4	—	—	31·1	4·5
Lean beef	72	19·3	—	—	3·6	5·1
Fat beef	51	14·8	—	—	29·8	4·4
Lean mutton	72	18·3	—	—	4·9	4·8
Fat mutton	53	12·4	—	—	31·1	3·5
Veal	63	16·5	—	—	15·8	4·7
Fat pork	39	9·8	—	—	48·9	2·3
Poultry	74	21·0	—	—	3·8	1·2
White Fish	78	18·1	—	—	2·9	1·0
Eels	75	9·9	—	—	13·8	1·3
Salmon	77	16·1	—	—	5·5	1·4
White of egg	78	20·4	—	—	—	1·6
Yelk of egg	52	16·0	—	—	30·7	1·3
Butter and Fat	15	—	—	—	83·0	2·0
Beer and porter	91	0·1	—	8·7	—	0·2

CLASSIFICATION OF THE ANIMAL KINGDOM.

VERTEBRATA.

MAMMALIA	*Typical Examples.*
Primates	Man.
,,	Ape, baboon.
Chiroptera	Bat, flying fox.
Insectivora	Mole, hedgehog.
Carnivora	Lion, dog, bear, seal.
Proboscidea	Elephant.
Hyracoidea	Hyrax.
Ungulata :	
Perissodactyla	Tapir, rhinoceros, horse.
Artiodactyla	Hippopotamus, pig, camel, chevrotain, deer, ox, sheep, goat, giraffe.
Sirenia	Dugong, manatee.
Cetacea	Whale, porpoise, narwhal.
Rodentia	Hare, porcupine, guinea pig, rat, beaver, squirrel, dormouse.
Edentata	Armadillo, pangolin, true anteater, Cape anteater, sloth.
Marsupiata	Opossum, bandicoot, Thylacinus, phalanger, wombat, kangaroo.
Monotremata	Ornithorhynchus or duck-billed platypus, Echidna or spiny anteater.
BIRDS	
CARINATÆ	
Raptores (*Birds of prey*)	Vulture, hawk, owl.
Scansores (*Climbing Birds*)	Woodpecker, parrot.
Passeres (*Perching Birds*)	Crow, finch, swallow.
Rasores (*Scratching Birds*)	Fowl, pheasant, grouse.
Grallatores (*Wading Birds*)	Heron, stork, snipe, crane.
Natatores (*Swimming Birds*)	Penguin, duck, pelican, gull.
RATITÆ	
Cursores (*Running Birds*)	Ostrich, emeu, apteryx.
REPTILES	
Crocodilia	Crocodile, alligator.
Lacertilia	Iguana, chameleon, gecko, lizard, slow-worm, flying dragon.
Chelonia	Tortoise, turtle.
Ophidia	Snake, viper.
AMPHIBIA	
Anura	Frog, toad.
Urodela	Newt, salamander.
FISH	
Dipnoi	Lepidosiren.
Teleostei	Perch, mackerel, cod, herring.
Placoidei	Shark, ray.
Ganoidei	Sturgeon, bony pike.
Cyclostomi	Lamprey, hag.
Leptocardii	Amphioxus lanceolatus.

CLASSIFICATION OF THE ANIMAL KINGDOM.

INVERTEBRATA.

MOLLUSCA	*Typical Examples.*
Cephalopoda	Octopus, argonaut, squid, cuttle-fish nautilus.
Pteropoda	Clio, Cleodora.
Gasteropoda:	
Pulmonigasteropoda	Snail, slug.
Branchiogasteropoda	Whelk, limpet, periwinkle.
Lamellibranchiata	Oyster, mussel, cockle.
Brachiopoda	Terebratula, Lingula.
Tunicata, or Ascidioidea.	Salpa, Pyrosoma.
Bryozoa or Polyzoa	Sea mat.
ARTHROPODA	
Insecta	Beetle, bee, ant, locust, grasshopper, cockroach, earwig, moth, butterfly, fly, flea. bug.
Arachnida	Scorpion, spider, mite.
Myriopoda	Centipede, millipede.
Crustacea	Crab, lobster, crayfish, prawn, barnacle.
Annulata	Sea-mouse, leech, earthworm.
Scolecida	Hair-worm, thread-worm, round-worm, fluke, tape-worm, guinea-worm.
Echinodermata	Sea-cucumber, sea-urchin, star-fish, sand-star, feather-star.
CŒLENTERATA	
Ctenophora	Beroe.
Anthozoa	Sea anemone, coral, sea-pen.
Hydrozoa	Hydra, Sertularia, Velella, Portuguese man-of-war.
Spongida	Sponges.
PROTOZOA	
Rhizopoda	Foraminifera, Amœba.
Infusoria	Paramœcium, Vorticella.

INDEX.

A.

- Abdominal muscles, action of in respiration, 232
- Aberration,
  - chromatic, 711
  - spherical, 710
- Abomasum, 296
- Absorbents. *See* Lymphatics.
- Absorption, 361
  - by blood-vessels, 377
  - by lacteal vessels, 375
  - by lymphatics, 376
  - conditions for, 380
  - by the skin, 426
  - oxygen by lungs, 241
  - process of osmosis, 378
  - rapidity of, 379
  - *See* Chyle, Lymph, Lymphatics, Lacteals.
- Accessory nerve, 635
- Accidental elements in human body, 860
- Accommodation of eye, 703
- Acids, organic, 856
  - acetic, *ib.*
- Acid-albumin, 305, 846
- Acini of secreting glands, 399
- Actinic rays, 724
- Addison's disease, 471
- Adenoid tissue, 40
- Adipose tissue, 42. *See* Fat.
  - development, 44
  - situations of, *ib.*
  - structure of, *ib.*
- Adrenals, 469
- After-birth, 778
- After-sensations,
  - taste, 666
  - touch, 658
  - vision, 715
- Aggregate glands, 399
- Agminate glands, 319
- Air,
  - atmospheric, composition of, 238
  - breathing, 234
  - complemental, *ib.*
  - reserve, *ib.*
- Air, *continued.*
  - residual, 234
  - tidal, *ib.*
  - changes by breathing, 239
  - quantity breathed, 235
  - transmission of sonorous vibrations through, 679, 680
  - in tympanum, for hearing, 682
  - undulations of, conducted by external ear, 679, 680
- Air-cells, 224
- Air-tubes, 220. *See* Bronchi.
- Alanines, 848
- Albino-rabbits, 24
- Albumin, 845
  - acid, 305
    - action of gastric fluid on, *ib.*
    - alkali, 845, 846
  - characters of, *ib.*
  - chemical composition of, 845
  - derived, 846
  - egg, 845
  - native, *ib.*
  - serum, 106, 845
  - tissues and secretion in which it exists, *ib.*
  - of blood, 102
- Albuminoids, 845
- Albuminose, 847
- Albuminous substances,
  - absorption of, 354
  - action of gastric fluid on, 305
    - of liver on, 348
    - of pancreas on, 330
- Alcoholic drinks, effect on respiratory changes, 240
- Alimentary canal, 277
  - development of, 806
  - length in different animals, 352
- Allantoin, 851
- Allantois, 769, 770
- Alloxan, 851
- Aluminium, 860
- Amic acids, 848
- Amides, *ib.*

- Ammonia,
  - cyanate of, identical with urea, 442, 850
  - exhaled from lungs, 242
  - urate of, 444
- Amnion, 769
  - fluid of, 770
- Amœba, 8
- Amœboid movements, 9, 475
  - cells, 35
  - colourless corpuscles, 99
  - cornea-cells, 34
  - ovum, 758
  - protoplasm, 8
  - Tradescantia, *ib.*
- Amphioxus, 779
- Ampulla, 675
- Amputation, sensations after, 556
- Amyloids or Starches, 855
  - action of pancreas and intestinal glands, 331, 352
    - of saliva on, 285
- Amylopsin, 331, 853
- Anacrotic wave, 182
- Anastomoses of muscular fibres of heart, 133
  - of nerves, 546
  - of veins, 201
  - in erectile tissues, 210
- Anelectrotonus, 516
- Angle, optical, 720
- Angulus opticus seu visorius, *ib.*
- Animal heat, 382. *See* Heat and Temperature.
- Animals, distinctive characters, 3
- Antialbumate, 847
- Antialbumose, *ib.*
- Antihelix, 672
- Antipeptone, 847
- Antitragus, 672
- Anus, 276
- Aorta, 159
  - development, 791
  - pressure of blood in, 189
  - valves of, 136
    - action of, 141
- Aphasia, 612
- Apnœa, 258. *See* Asphyxia.
- Appendices epiploicæ, 325
- Appendix vermiformis, *ib.*
- Aquæductus,
  - cochleæ, 676
  - vestibuli, 675
- Aqueous humour, 700
- Arches, visceral, 782
- Area germinativa, 761
  - opaca, 762
  - pellucida, *ib.*
  - vasculosa, 768
- Areolar tissue, 37. *See* Connective Tissue.
- Arsenic, 860
- Arterial tension, 185
- Arteries, 159
  - circulation in, 171
    - velocity of, 204
  - distribution, 159
  - muscular contraction of, 175
  - effect of cold on, 176
    - of division, *ib.*
  - elasticity, 172
    - purposes of, *ib.*
  - muscularity, 160
    - governed by nervous system, 190
    - purposes of, 175
  - nerves of, 164
  - nervous system, influence of, 190
  - office of, *ib.*
  - pressure of blood in, 185
  - pulse, 177. *See* Pulse.
  - rhythmic contraction, 174
  - structure, 160
    - distinctions in large and small arteries, *ib.*
  - systemic, 126
  - tone of, 190
  - umbilical, 793
  - velocity of blood in, 204
- Articulate sounds, classification of, 530. *See* Vowels and Consonants.
- Arytenoid cartilages, 521
    - effect of approximation, 523
    - movements of, *ib.*
  - muscle, 521
- Asphyxia, 259
  - causes of death in, *ib.*
  - experiments on, 260
- Astigmatism, 710
- Atmospheric air, 238. *See* Air.
  - pressure in relation to respiration, 239
- Auditory canal, 672
  - function, 679
- Auditory nerve, 678
  - distribution, *ib.*
  - effects of irritation of, 690
- Auricle of ear, 672
- Auricles of heart, 128, 130
  - action, 137
  - capacity, 132
  - development, 789
  - dilatation, 153
  - force of contraction, *ib.*
- Automatic action, 563,
  - cerebrum, 608
  - medulla oblongata, 588
  - respiratory, 588, 589
- Axis-cylinder of nerve-fibre, 542

B.

- Barytone voice, 527
- Basement-membrane,
  - of mucous membranes, 397
  - of secreting membranes, 394

Bass voice, 526
Battery, Daniell's, 490
Benzoic acid, 458
Bicuspid valve, 135
Bile, 338
  antiseptic power, 347
  colouring matter, 340
  composition of, 338
  digestive properties, 346
  excrementitious, 343
  fat made capable of absorption by, 346
  functions in digestion, *ib.*
  mixture with chyme, 347
  mucus in, 341
  natural purgative, 347
  process of secretion of, 342
  quantity, 343
  re-absorption, 342, 347
  salts, 339
  secretion and flow, 342
  secretion in fœtus, 344
  tests for, 340, 341
  uses, 343
Bilifulvin, Biliprasin, Bilirubin, Biliverdin, 340
Bilin, 339
  preparation of, 339
  re-absorption of, 342, 347
Bioplasm, 6. *See* Protoplasm
Birth, 1
Bladder, urinary, 430. *See* Urinary Bladder
Blastema, 6. *See* Protoplasm
Blastodermic membrane, 760
Bleeding, effects of, on blood, 107
Blind spot, 713
Blood, 78
  albumin, 106
    use of, 123
  arterial and venous, 108
  assimilation, 123
  buffy coat, 82
  chemical composition, 102
  coagulation, 80
  colour, 78, 108
    changed by respiration, 245
  colouring matter, 103, 112
  colouring matter, relation to that of bile, 341
  composition, chemical, 102
    variations in, 108
  corpuscles or cells of, 92. *See* Blood-corpuscles.
    red, 92
    white, 98
  crystals, 112
  cupped clot, 82
  development, 119
  extractive matters, 106
  fatty matters, *ib.*
    use of, 123
  fibrin, 81, 104
Blood, *continued.*
    separation of, 81
    use of, 123
  formation in liver, 102
    in spleen, 464
  gases of, 109
  hæmoglobin or cruorin, 103, 112
  hepatic, 108
  menstrual, 745
  odour or halitus of, 78
  portal, characters of, 108
    purification of by liver, 343
  quantity, 79
  reaction, 78
  relation of, to lymph, 374
  saline constituents, 106
    uses of, 124
  serum of, 105
    compared with secretion of serous membrane, 395
  specific gravity, 78
  splenic, 108
  structural composition, 92
  temperature, 78
  uses, 123
    of various constituents, *ib.*
  variations of, in different circumstances, 107
    in different parts of body, 108
Blood-corpuscles, red, 92
  action of reagents on, 94
  chemical composition, 103
  development, 119, 120
  disintegration and removal, 122
  method of counting, 100
  rouleaux, 94
  sinking of, 82
  specific gravity, 93
  stroma, *ib.*
  tendency to adhere, 94
  uses, 124
  varieties, 93
  vertebrate, various, 95
Blood-corpuscles, white, 98
  amœboid movements of, 99
  derivation of, 122
  formation of, in spleen, 122, 464
  locomotion, 99
Blood-crystals, 112
Blood-pressure, 185
  influence of vaso-motor system of, 193
  variations, 189
Blood-vessels,
  absorption by, 377
    circumstances influencing, 380
    difference from lymphatic absorption, 378
    osmotic character of, 379
    rapidity of, *ib.*
  development, 786
  influence of nervous system on, 190
  relation to secretion, 403
Bone, 51

Bone, *continued.*
  canaliculi, 53
  cancellous, 51
  chemical composition, *ib.*
  compact, *ib.*
  development, 57
  functions, 67
  Haversian canals, 54
  lacunæ, 53
  lamellæ, 55
  medullary canal, 51
  periosteum, 52
  structure, 51
  growth, 66
Brain. *See* Cerebellum, Cerebrum, Pons, etc.
  adult, 607
  amphibia, 606
  apes, 607
  birds, 606
  capillaries of, 167, 208
  child, 607
  circulation of blood in, 208, *et seq.*
  convolutions, 601
  development, 799
  female, 607
  fish, 606
  gorilla, 607
  idiots, *ib.*
  lobes, 601
  male, 607
  mammalia, 606
  orang, 608
  proportion of water in, 858
  quantity of blood in, 208, *et seq.*
  rabbit, 607
  reptiles, 606
  weight, 607
    relative, *ib.*
Breathing, 214. *See* Respiration.
Breathing-air, 234
Bronchi, arrangement and structure of, 220
Bronchial arteries and veins, 226
Brownian movement, 8
Brunner's glands, 318
Buffy coat, formation of, 81
Bulbus arteriosus, 790
Burdach's column, 572
Bursæ mucosæ, 395

C.

Cæcum, 325
Calcification compared with ossification, 62
Calcium, 859
  fluoride, *ib.*
  phosphate, *ib.*
  carbonate, *ib.*
Calculi, biliary, containing cholesterin, 855,
  containing copper, 342
Calyces of the kidney, 428
Canal, alimentary, 276. *See* Stomach, Intestine, etc.
  external auditory, 672
    function of, 679
  spiral, of cochlea, 678
Canaliculi of bone, 53
Canalis membranaceus, 678
Canals, Haversian, 54
  portal, 334
  semicircular, 675
  function of, 685
Cancellous texture of bone, 51
Capacity of chest, vital, 235
  of heart, 132
Capillaries, 164
  circulation in, 197
    rate of, 206
  contraction of, 200
  development, 786
  diameter of, 165
  influence of on circulation, 200
  lymphatic, 363
  network of, 166
  number, 167
  passage of corpuscles through walls of, 199
  resistance to flow of blood in, 197
  still layer in, *ib.*
  structure of, 165
  of lungs, 166
  of stomach, 302
Capric acid, 856
Caproic acid, *ib.*
Capsule of Glisson, 332
Capsules, Malpighian, 429, 433
Carbonic acid in atmosphere, 238
  in blood, 109
  effect of, 252
  exhaled from skin, 425
  increase of in breathed air, 239
  in lungs, 244
  in relation to heat of body, 385
Carbonates, 859
Cardiac orifice of stomach, action of, 310
  sphincter of, *ib.*
    relaxation in vomiting, *ib.*
Cardiac revolution, 144
Cardiograph, 148
Carnivorous animals, food of, 272
  sense of smell in, 670
Cartilage, 46
  articular, *ib.*
  cellular, 49
  chondrin obtained from, 848
  classification, 46
  development, 50
  elastic, 49
  fibrous, *ib.* *See* Fibro-cartilage.
  hyaline, 46

Cartilage, *continued.*
  matrix, 47
  ossification, 62
  perichondrium of, 64
  structure, 46
  temporary, 48
  uses, 50
  varieties, 46
Cartilage of external ear, used in hearing, 679
Cartilages of larynx, 521
Casein, 845, 846. *See* Milk.
Cauda equina, 565
Caudate ganglion corpuscles, 551
Cause of fluidity of living blood, 90
Cells, 10
  abrasion, 17
  amœboid, 35
  blood, 92. *See* Blood-corpuscles
  cartilage, 46
  chemical transformation, 17
  ciliated, 29
  classification, 19
  contents of, 11
  decay and death, 17
  definition of, 10
  epithelium, 22. *See* Epithelium
  fission, 14, 15
  formative, 761
  functions, 16
  gemmation, 13
  gustatory, 664
  lacunar of bone, 53
  modes of connection, 19
  nutrition, 10
    action of, in secretion, 289
  olfactory, 668
  pigment, 24
  reproduction, 13
  segmentation, 14
  structure of, 10
  transformation, 17
  varieties, 18, 19
  vegetable, 8
    distinctions from animal cells, 4
Cellular cartilage, 49
Cement of teeth, 71
Centres, nervous, 191, 193, &c. *See* Nerve-centres
  of ossification, 66
Centrifugal nerve-fibres, 554
Centripetal nerve-fibres, *ib.*
Cerebellum, 595
  co-ordinating function of, 598
  cross-action of, 599
  effects of injury of crura, *ib.*
    of removal of, 597
  functions of, *ib.*
  in relation to sensation, *ib.*
    to motion, *ib.*
    to muscular sense, 598
    to sexual passion, *ib.*
  structure of, 595
Cerebral circulation, 208
  hemispheres, 600. *See* Cerebrum
Cerebral nerves, 619
  third, 620
    effects of irritation and injury of, *ib.*
    relation of to iris, *ib.*
  fourth, 621
  fifth, 622
    distribution of, *ib.*
    effect of division of, *ib.*
    influence of on iris, 625
        on muscles of mastication, 622
        on organs of special sense, 624, *et seq.*
  relation of, to nutrition, 625
  resemblance to spinal nerves, 622
  sensory function of greater division of fifth, 622
  sixth, 627
    communication of, with sympathetic, 628
  seventh, *ib.* *See* Auditory Nerve *and* Facial Nerve
  eighth, 630, *et seq.* *See* Glosso-pharyngeal, Pneumogastric, *and* Spinal Accessory Nerves
  ninth, 635
Cerebration, unconscious, 611
Cerebrin, 850
Cerebro-spinal fluid, relation to circulation, 209
Cerebro-spinal nervous system, 564, *et seq.*
  See Brain, Spinal Cord, &c.
Cerebrum, its structure, 600, 604
  chemical composition, 606
  convolutions of, 601, *et seq.*
  crura of, 590
  development, 799
  distinctive character in man, 607
  effects of injury, 609
  electrical stimulation, 613
  functions of, 608
  grey matter, 604
  in relation to speech, 612
  localization of functions, 610
  structure, 604, *et seq.*
  unilateral action of, 610
  white matter, 605
Cerumen, or ear-wax, 417
Chalk-stones, 444
Characteristics of organic compound, 844
Charcoal, absorption of, 381
Chemical composition of the human body, 844—860
Chest, its capacity, 235
  contraction of in expiration, 321
  enlargement of in inspiration, 228
Chest-notes, 528
Cheyne-Stokes' breathing, 258
Chlorine, 859

Chlorine, *continued.*
  in human body, 859
  in urine, 449
Cholesterin, 855
  in bile, 341
Chondrin, 848
Chorda dorsalis, 764
Chorda tympani, 286 *et seq.*
Chordæ tendineæ, 135
  action of, 139
Chorion, 771
  villi of, 772
Choroid coat of eye, 694
  blood-vessels, 699
Choroidal fissure, 804
Chromatic aberration, 711
Chyle, 373
  absorption of, 375
  analysis of, 374
  coagulation of, *ib.*
  compared with lymph, 373
  corpuscles of, 374. *See* Chyle-corpuscles
  course of, 361
  fibrin of, 374
  forces propelling, 375
  molecular base of, 373
  quantity found, 375
  relation of, to blood, *ib.*
Chyle-corpuscles, 374
Chyme, 305
  absorption of digested parts of, 353
  changes of in intestines, 353, *et seq.*
Cilia, 29, 474
Ciliary epithelium, 29
  of air passages, 220
  function of, 30
Ciliary motion, 30, 474
  nature of, 475
Ciliary-muscles, 702
  action of in adaptation to distances, 705
Ciliary processes, 694
Circulation of blood, 124
  action of heart, 137
  agents concerned in, 211
  arteries, 171
  brain, 208
  capillaries, 197
  course of, 124, *et seq.*
  discovery, 212
  erectile structures, 210
  fœtal, 796
  forces acting in, 127
  influence of respiration on, 253
  peculiarities of, in different parts, 208
  portal, 334
  proofs, 212
  pulmonary, 244
  systemic, 126
  in veins, 201
    velocity of, 203
Circumvallate papillæ, 661
Claviculi of Gagliardi, 57
Cleft, ocular, 804
Clefts, visceral, 782
Clitoris, 742
  development of, 818
Cloaca, 816
Clot or coagulum of blood, 81
  See Coagulation.
  of chyle, 374
Coagulation of blood, 81
    absent or retarded, 88
    conditions affecting, *ib.*
    influence of respiration on, 245
    theories of, 87
  of chyle, 374
  of lymph, *ib.*
Coat, buffy, 81
Coats of arteries, 101
Cochlea of the ear, 671
  office of, 682
Cold-blooded animals, 384
  extent of reflex movements in, 577
  retention of muscular irritability in, 504
Colloids, 379
Colon, 325
Colostrum, 408
Colour-blindness, 726
Colouring matter,
  of bile, 340
  of blood, 103, 112
  of urine, 446
Colours, optical phenomena of, 723, *et seq.*
Columnæ carneæ, 130
  action of, 136
Columnar epithelium, 28
Complemental air, 234
  colours, 725
Compounds, 843
  inorganic, 857
  organic, 843
Concha, 672
  use of, 679
Cones of retina, 697
Coni vasculosi, 751
Conjunctiva, 691
Connective tissues, 33
  corpuscles of, *ib.*
  fibrous, 37
  gelatinous, 39
  retiform, 40
  varieties, 38
Consonants, 532
  varieties of, *ib.*
Contralto voice, 526
Convolutions, cerebral, 601, *et seq.*
Co-ordination of movements, office of cerebellum in, 598
  office of sympathetic ganglia in, 642
Copper, an accidental element in the body, 860

Copper, *continued.*
  in bile, 342
Cord, spinal, 565. *See* Spinal Cord
  umbilical, 778
Cords, tendinous, in heart, 135
  vocal, 520. *See* Vocal Cords.
Corium, 413
Cornea, 693
  action of on rays of light, 700
  corpuscles, 693
  nerves, *ib.*
  structure, *ib.*
  after injury of fifth nerve, 626
Corpora Arantii, 136
  geniculata, 592
  quadrigemina, *ib.*
    their function, *ib.*
  striata, 593
    their function, 594
Corpus callosum, office of, 615
  cavernosum penis, 210
  dentatum
    of cerebellum, 596
    of olivary body, 587
  luteum, 747
    of human female, 747
    of mammalian animals, *ib.*
    of menstruation and pregnancy compared, 750
  spongiosum urethræ, 210
Corpuscles of blood, 92. *See* Blood-corpuscles.
  of chyle, 374
  of connective tissue, 33
  of cornea, 693
  of lymph, 374
  Pacinian, 547
Correlation of life with other forces, 818
Cortical substance of kidney, 428
  of lymphatic glands, 369
Corti's rods, 677
  office of, 687
Costal types of respiration, 232
Coughing, influence on circulation in veins, 256
  mechanism of, 248
  sensation in larynx before, 559
Cowper's glands, 750
  office uncertain, 756
Cranial nerves. 619. *See* Cerebral nerves.
Cranium, development of, 799
Crassamentum, 81
Crescents of Gianuzzi, 281. *See* Semilunes of Heidenhain.
Crico-arytenoid muscles, 521
Cricoid cartilages, *ib.*
Crossed pyramidal tract, 572
Crura cerebelli,
    effect of dividing, 598, *et seq.*
      of irritating, *ib.*
  cerebri, 590
    their office, 591
Crusta petrosa, 71
Cryptogamic plants, movements of spores of, 4
Crystal growth of, 2
Crystallin, 846
Crystalline lens, 700
    in relation to vision at different distances, 704
Crystalloids, 379
  blood, 112
Cubic feet of air for rooms, 253
Cupped appearance of blood-clot, 82
Curdling ferments, 307, 854
Currents of action, 502
  ascending, 515
  continuous, 490
  descending, 515
  induced, 492
  muscle, 487
  natural, 488
  negative variation, 502
  nerve, 513
  polarising, 515
  rest, 488, 513
Curves, Traube-Hering's, 258
Cuticle, 410. *See* Epidermis, Epithelium.
  of hair, 419
Cutis anserina, 476
  vera, 413
Cyanate of ammonium, 442
Cylindrical or columnar epithelium, 28
Cystic duct, 332
Cystin in urine, 449

D.

Daltonism, 726
Daniell's battery, 490
Decidua,
  menstrualis, 745
  reflexa, 775
  serotina, *ib.*
  vera, 774
Decline, 3
Decomposition, tendency of animal compounds to, 844
Decomposition-products, 848
Decussation of fibres in medulla oblongata, 585
    in spinal cord, 576
  of optic nerves, 732
Defæcation, mechanism of, 357
  influence of spinal cord on, 581
Deglutition, 291. *See* Swallowing.
Dentine, 67
Depressor nerve, 192
Derived albumins, 846
Derma, 413
Descendens noni nerve, 635
Descemet's membrane, 693

Development, 3, 757
    of organs, 778
  alimentary canal, 806
  arteries, 791
  blood, 119, *et seq.*
  blood-vessels, 786
  bone, 57
  brain, 799
  capillaries, 786
  cranium, 799
  ear, 805
  embryo, 761
  extremities, 784
  eye, 802
  face and visceral arches, 782
  heart, 785
  liver, 809
  lungs, *ib.*
  medulla oblongata, 801
  muscle, 483
  nerves, 798
  nervous system, *ib.*
  nose, 806
  organs of sense, 802
  pancreas, 808
  pituitary body, 781
  respiratory apparatus, 810
  salivary glands, 808
  spinal cord, 798
  teeth, 71
  vascular system, 785
  veins, 793
  vertebral column and cranium, 778
  visceral arches and clefts, 782
  of Wolffian bodies, urinary apparatus and sexual organs, 810
Dextrin, 285
Diabetes, 351
Diamides, 848
Diapedesis of blood-corpuscles, 198
Diaphragm,
  action of, on abdominal viscera, 218
    in inspiration, 228
    in various respiratory acts, 245
    in vomiting, 310
Diaphysis, 66
Diastole of heart, 137
Dicrotous pulse, 182
Diet—
  daily, 272
  influence on blood, 107
  mixed, necessity of, 263, *et seq.*
Diffusion of gases in respiration, 244
Digestion, 276
  in the intestines, 352, 355
  in the stomach, 305
  influence of nervous system on, 360
  of stomach after death, 313
  See Gastric fluid, Food, Stomach.
Diplopia, 729
Direct cerebellar tract, 572
  pyramidal tract, 571
Direction of sounds, perception of, 688
Discus proligerus, 739
Disdiaclasts, 479
Distance, adaptation of eye to, 703
  of sounds, how judged of, 689
Distinctness of vision, how secured, 699, *et seq.*
Dormant vitality, 821
Dorsal laminæ, 762, 782
Double hearing, 690
  vision, 730
Dreams, 618
Drowning, cause of death in, 261
Duct, cystic, 332
  hepatic, 336
  thoracic, 361
  vitelline, 767
Ductless glands, 461
Ducts of Cuvier, 795
Ductus arteriosus, 792
  venosus, 795, 796
  closure of, 798
Duodenum, 315
Duration of impressions on retina, 714
Duverney's glands, 793
Dysphagia, absorption from nutritive baths in, 427
Dyspnœa, 259

E.

Ear, 671
  bones or ossicles of, 673
    function of, 682
  development of, 805
  external, 672
  function of, 679
  internal, 674
    function of, 685
  middle, 673
    function of, 680
Ectopia vesicæ, 459
Efferent nerve-fibres, 554
  lymphatics, 372
  vessels of kidney, 433
Egg-albumin, 845
Eighth cranial nerve, 630
Elastic cartilage, 49
  fibres, 36
  tissue, 39
Elastin, 848
Electricity,
  in muscle, 485
    nerve, 513
    retina, 717
Electrodes, 486
Electrotonus, 515
Elementary substances in the human body, 843
  accidental, 860
Embryo, 761, *et seq.* *See* Development and Fœtus, formation of blood in, 119
Emmetropic eye, 708

Emotions, connection of with cerebral hemispheres, 608
Enamel of teeth, 70
Enamel organ, 71
End-bulbs, 416
End-plates, motorial, 549
Endocardium, 134
Endolymph, 674
  function of, 685
Endomysium, 478
Endoneurium, 541
Endosmometer, 378
Endothelium, 24
  distinctive characters, *ib.*
  germinating, 27
Energy, 536
  relations of vital to physical, chap. xx.
  daily amount expended in body, 536
Epencephalon, 801
Epiblast, 760
Epidermis, 411
  development, etc., of, 412
  functions of, 422
  hinders absorption, 413
  pigment of, 412
  relation to sensibility, 423
  structure of, 411
  thickening of, 412
Epididymis, 751
Epiglottis, 520
  action in swallowing, 294
  influence of on voice, 524
Epineurium, 541
Epiphysis, 66
Epithelium, 22
  air-cells, 225
  arteries, 161
  bronchi, 220
  bronchial tubes, *ib.*
  ciliated, 29
  cogged, 24
  columnar, 28
  cylindrical, *ib.*
  development, 32
  glandular, 27
  goblet-shaped, 29
  growth, 32
  mucous membranes, 397
  olfactory region, 668
  secreting glands, 399
  serous membranes, 394
  spheroidal, 27
  squamous or tesselated, 23
  transitional, 30
Erect position of objects, perception of, 718
Erectile structures, circulation in, 210
Erection, *ib.*
  cause of, *ib.*
  influence of muscular tissue in, *ib.*
  a reflex act, 581
Erythro-granulose, 583
Erythro-dextrin, 853
Eunuchs, voice of, 527
Eustachian tube, 673
  development, 806
  function of, 684
Eustachian valve, 129
Excito-motor and sensori-motor acts, 560
Excreta in relation to muscular action, 512, *et seq.*
Excretin, 356
Excretion, 427
Excretoleic acid, 356
Exercise,
  effects of, on production of carbonic acid, 240
    on temperature of body, 383
    on venous circulation, 202
Expenditure of body, 534
  amount, 534
  compared with income, 535
  evidences, 534
  objects, 536
  sources, *ib.*
Expiration, 231
  influence of, on circulation, 255
  mechanism of, 231
  muscles concerned in, 232
  relative duration of, 233
Expired air, properties of, 239, *et seq.*
Extractive matters,
  in blood, 106
  in urine, 447
Extremities, development of, 784
Eye, 691
  adaptation of vision at different distances, 699, *et seq.*
  blood-vessels, 698
  capillary vessels of, 694
  development of, 802
  effect on, of injury of facial nerve, 628
    of fifth nerve, 625, 627
  effect of pressure on, 730
  nerves, supplying muscles of, 620, 621, 627
  optical apparatus of, 699
  refracting media of, 700
  resemblance to camera, 712
  structure of, 692
Eyelids, 691
  development of, 805
Eyes, simultaneous action of in vision, 729

F.

Face, development of, 782
  effect of injury of seventh nerve on, 628
Facial nerve, 628
  effects of paralysis of, *ib.*

Facial nerve, *continued.*
  relation of, to expression, 628
Fæces, composition of, 356
  quantity of, *ib.*
Fallopian tubes, 741
  opening into abdomen, *ib.*
Falsetto notes, 528
Fasciculus,
  cuneatus, 572
  olivary, *ib.*
  teres, *ib.*
Fasting,
  influence on secretion of bile, 342
Fat. *See* Adipose tissue.
  action of bile on, 346
    of pancreatic secretion on, 331
    of small intestine on, 353
  absorbed by lacteals, 375
  formation of, 538
  in blood, 106
  in relation to heat of body, 390
  of bile, 341
  of chyle, 374
  situations where found, 42
  uses of, 45
Fechner's law, 715
Female generative organs, 736
Fenestra ovalis, 674
  rotunda, 675
Ferments, 85, 285, 305, 330, 331
Fibres, 20
  of Müller, 698
Fibrils or filaments, 20
Fibrin, 847, in blood, 81
    use of, 123
  in chyle, 374
  formation of, 81
  in lymph, 374
  sources and properties of, 847
  vegetable, 267
Fibrinogen, 84, *et seq.*
Fibrinoplastin, *ib.*
Fibro-cartilage, 49
  classification, *ib.*
  development, *ib.*
  uses, *ib.*
  white, *ib.*
  yellow, *ib.*
Fibrous tissue, 37
  white, 37
  yellow, 38
  development, 40
Field of vision, actual and ideal size of, 719
Fifth nerve, 622. *See* Cerebral Nerves.
Fillet, 584
Filtration, 401
Filum terminale, 565
Fimbriæ of Fallopian tube, 741
Fingers, development of, 784
Fish,
  temperature of, 384
Fissures,
  of brain, 601, *et seq.*
  of spinal cord, 566
Fistula, gastric, experiments in cases of, 303, 304
Flesh, of animals, 265
Fluids, passage of, through membranes, 378
Fluoride of calcium, 859
Focal distance, 703
Fœtus,
  blood of, 119
  circulation in, 796
  communication with mother, 776
  fæces of, 344
  membranes, 767
  office of bile in, *ib.*
  pulse in, 151
Folds, head and tail, 765
Follicles, Graafian, 738. *See* Graafian Vesicles.
Food, 262—276
  albuminous, changes of, 305
  amyloid, changes of, 285, 331, 354
  of animals, 272
  of carnivorous animals, *ib.*
  classification of, 264
  composition of many, 845, *et seq.*
  digestibility of articles of, 307
    value dependent on, 275
  digestion of, in intestines, 353, *et seq.*
    in stomach, 307, *et seq.*
  improper, 272
  of man, 263
  mixed, the best for man, 263
  mixture of, necessary, 264
  relation of, to carbonic acid produced, 240
    to heat of body, 385
    to muscular action, 512
  relation of, to urea, 456
    to urine, 440
      phosphates in, 448
      table of, 275
      too little, 269
      too much, 273
  vegetable, contains nitrogenous principles, 267
Foot-pound, 154
Foot-ton, *ib.*
Foramen ovale, 130
Forced movements, 599
Form of bodies, how estimated, 721
Formation of fat, 538
Formic acid, 856
Fornix, office of, 616
Fourth cranial nerve, 621
  ventricle, 584
Fovea centralis, 713
Fundus of bladder, 436

Fundus of uterus, 741
Fungiform papillæ of tongue, 662

G.

Galactophorous ducts, 406
Gall-bladder, 337
  functions, 338
  passage of bile into and from, 342
  structure, 337
Ganglia. *See* Nerve centres.
  of spinal nerves, 569
  of the sympathetic, 637
    action of, 640, *et seq.*
    as co-ordinators of involuntary movements, 642
    structure of, 637
  in heart, 155
  in substance of organs, 642
Ganglion, Gasserian, 622
  corpuscles, 550
    See Nerve-corpuscles.
Gases, 843
  in bile, 341
  in blood, 109
  extraction of, *ib.*
  extraction from blood, *ib.*
  in stomach and intestines, 367
  in urine, 450
Gastric glands, 299
Gastric juice, 303
  acid in, 304
  action of, on nitrogenous food, 305
    on non-nitrogenous food, 307
    on saccharine and amyloid principles, *ib.*
  artificial, 305
    preparation of, *ib.*
  characters of, 303
  composition of, 304
  digestive power of, 305
  experiments with, *ib.*
  pepsin of, *ib.*
  quantity of, 304
  secretion of, 303
    how excited, *ib.*
    influence of nervous system on, 312
Gelatin, 847
  as food, 273
  action of gastric juice on, 307
  action of pancreatic juice on, 331
Gelatinous substances, 847
Generation and development, 736
Generative organs of the female, *ib.*
  of the male, 750
Genito-urinary tract of mucous membrane, 397
Gerlach's network, 568
Germinal area, 761
  epithelium, 737
  matter, 6. *See* Protoplasm.
Germinal membrane, 760
  spot, 740
    development, *ib.*
  vesicle, *ib.*
    development of, *ib.*
  disappearance of, 758
Gill, 214
Gizzard, action of, 297
Gland, pineal, 472
  pituitary, *ib.*
  prostate, 750, 756
Gland-cells, agents of secretion, 402
  changes in during secretion, 289, 301, 328
  relation to epithelium, 398
Gland-ducts, arrangement of, 402
  contractions of, 403
Glands, aggregate, 399
  Brunner's, 318
  ceruminous, 417
  Cowper's, 750
  ductless, 461. *See* vascular.
  Duverney's, 743
  of large intestine, 326
  of Lieberkühn, 317
  lymphatic, 368. *See* Lymphatic Glands.
  mammary, 405
  of Peyer, 318
  salivary, 279
  sebaceous, 417
  secreting, 398. *See* Secreting Glands.
  of small intestines, 317
  of stomach, 299
  sudoriferous, 416
  tubular, 399
  vascular, 461. *See* Vascular Glands.
  vulvo-vaginal, 743
Glandula Nabothi, 742
Glisson's capsule, 332
Globulin, 106, 846
  distinctions from albumin, 846
Globus major and minor, 751
  development, 812
Glosso-pharyngeal nerve, 285, 630
  communications of, *ib.*
  motor filaments in, *ib.*
  a nerve of common sensation and of taste, 630
Glottis, action of laryngeal muscles on, 522
  closed in vomiting, 311
  effect of division of pneumogastric nerves on, 634
  forms assumed by, 523
  narrowing of, proportioned to height of note, 524
  respiratory movements of, 234
Glucose, 856
  in liver, 350
  test for, 284
Gluten in vegetables, 267
Glycerin extract, 305, 329

Glycin, 849
Glycocholic acid, *ib.*
Glycogen, 350, 855
  characters, 350
  destination, 349
  preparation, 350
  quantity formed, 349
  variation with diet, *ib.*
Glycosuria, 351
  artificial production of, *ib.*
Goll's column, 572
Graafian vesicles, 738
  formation and development of, 738, *et seq.*
  relation of ovum to, 739
  rupture of, changes following, 743
Granular layers of retina, 694
Grape-sugar, 856. *See* Glucose.
Grey matter of cerebellum, 595
  of cerebrum, 604
  of crura cerebri, 590
  of medulla oblongata, 587
  of pons Varolii, 590
  of spinal cord, 568
Groove, primitive, 762
Growth, 2,
  coincident with development, 3
  of bone, 66
  not peculiar to living beings, 2
Guanin, 851
Gubernaculum testis, 815
Gullet, 292
Gustatory nerves, 659
  cells, 664

H.

Habitual movements, 562
Hæmatin, 110
  hydrochlorate of, 117
Hæmadynamometer, 186
Hæmatochometer, 206
Hæmatoidin, 116
Hæmin, 117
Hæmocytometer, 101
Hæmoglobin, 112, *et seq.*
  action of gases on, 115
  distribution, 118
  estimation of, 118
  spectrum, 114
Hair-follicles, 420
  their secretion, 423
Hairs, 418
  chemical composition of, 848
  structure of, 418
Hamulus, 676
Hare-lip, 783
Hassall, concentric corpuscles of, 467
Haversian canals, 54
Hearing, anatomy of organ of, 671
Hearing, *continued.*
  double, 690
  impaired by lesion of facial nerve, 629
  influence of external ear on, 672
    of labyrinth, 685
    of middle ear, 680
  physiology of, 678
  See Sound, Vibrations, etc.
Heart, 127-159
  action of, 137
    accelerated, 158
    effects of, 153
    force of, 151
    frequency of, *ib.*
    inhibited, 157
    after removal, *ib.*
    rhythmic, 155
    work of, 154
  auricles of 128, 137
    See Auricles.
  capacity, 132
  chambers, 128
  chordæ tendineæ of, 135
  columnæ carnæ of, 130, 136
  course of blood in, 134
  development, 785
  endocardium, 128
  force, 181
  frog's, 154
  ganglia of, 155
  impulse of, 147
    tracing by cardiograph, 148, *et seq.*
  influence of pneumogastric nerve, 156
    of sympathetic nerve, 158
  investing sac, 127
  muscular fibres of, 132
  musculi papillares, 135, 140
  nervous connections with other organs, 157
    rhythm, 156
  nervous system, influence on, 154
  revolution of, 144
  situation, 127
  sounds of, 145
    causes, 146
  structure of, 132
  tendinous cords of, 135
  tubercle of Lower in, 129
  valves, 135
    arterial or semilunar, 136
      function of, 141
    auriculo-ventricular, 135
      function of, 139
  ventricles, their action, 138
    capacity, 132
  weight of, *ib.*
  work of, 154
Heat, animal, 382. *See* Temperature.
    influence of nervous system, 390
      of various circumstances on, 382, *et seq.*
    losses by radiation, etc., 387
    in relation to bile, 345

- Heat, *continued.*
  - sources and modes of production, 386
  - developed in contraction of muscles, 382, 386,
  - perception of, 656
- Heat centres, 391
- Heat-producing tissues, 386
- Heat or rut, 743
  - analogous to menstruation, *ib.*
- Height, relation to respiratory capacity, 235
- Helicotrema, 676
- Helix of ear, 672
- Hemipeptone, 847
- Hemispheres, Cerebral, 600. *See* Cerebrum
- Hepatic cells, 333
  - ducts, 336
  - veins, 335
    - characters of blood in, 108
  - vessels, arrangement of, 334, *et seq.*
- Herbivorous animals,
  - perception of odours by, 670
- Hering's theory, 724
- Hermaphroditism, apparent, 818
- Hiccough, mechanism of, 247
- Hip-joint, pain in its diseases, 559
- Hippuric acid, 446, 458, 849
- Horse's blood, peculiar coagulation of, 82
- Howship's lacunæ, 53
- Hunger, sensation of, 270
- Hyaline cartilage, 46
- Hybernation, state of thymus in, 468
- Hydrogen, 843
- Hydrolytic ferments, 284, 852
- Hymen, 742
- Hyperæsthesia,
  - result of injury to spinal cord, 576
- Hypermetropia, 709
- Hypoblast, 760
- Hypoglossal nerve, 635
- Hypospadias, 818
- Hypoxanthin, 851

I.

- Ideas, connection of, with cerebrum, 609
- Ileum, 315
- Ileo-cæcal valve, 326
- Illusions of touch, 655
- Image, formation of, on retina, 700
  - distinctness of, 708
  - inversion of, 717
- Impulse of heart, 147
- Income of body, 535
  - compared with expenditure, *ib.*
- Incus,
  - function of, 673
- Indican, 446
- Indigo, 852
- Indol, 330
- Induction
  - coil, 492
  - current, *ib.*
- Infundibulum, 224
- Inhibitory influence of pneumogastric nerve, 156
- Inhibitory action of brain, 579
  - nerves, 554
    - action of, on heart, 156
      - on blood-vessels, 193
      - on blood-vessels of salivary glands, 286, *et seq.*
      - on gastric blood-vessels, 312, *et seq.*
      - on intestinal movements, 359
      - on respiratory movements, 249
- Inhibitory heat-centre, 391
- Inorganic matter, distinction from organised, 844, *et seq.*
  - principles, 857
- Inosite, 856
- Insalivation, 279
- Inspiration, 227
  - elastic resistance overcome by, 236
  - extraordinary, 231
  - force employed in, 237
    - during dyspnœa, 259
  - influence of, on circulation, 253
  - mechanism of, 228
- Intercellular substance, 20
- Intercostal muscles, action in inspiration, 229, *et seq.*
  - in expiration, 231
- Interlobular veins, 336
- Intestinal juice, 351
- Intestines, digestion in, 352, 355
  - development, 807
  - fatty discharges from, 331
  - gases, 367
  - large, digestion in, 355
    - structure, 325
  - length in different animals, 352
  - movements, 359
  - small, changes of food in, 352
    - structure of, 315
- Intonation, 527, *et seq.*
- Intralobular veins, 336
- Inversive ferments, 352
- Involuntary muscles,
  - actions of, 311
  - structure of, 476
- Iris, 701
  - action of, 701, *et seq.*
    - in adaptation to distances, 705
  - blood-vessels, 701
  - development of, 805
  - influence of fifth nerve on, 702
    - of third nerve, *ib.*
  - relation of, to optic nerve, *ib.*
- Iron, 859
- Irradiation, 712

Ivory of teeth, 70

J.

Jacob's membrane, 697
Jacobson's nerve, 630
Jaw, interarticular cartilage, 278
Jejunum, 315
Juice, gastric, 303
  pancreatic, 330
Jumping, 511

K.

Karyokinesis, 15
Katacrotic wave, 182
Katelectrotonus, 516
Keratin, 307
Key, 491
Kidneys, their structure, 428
  blood-vessels of, how distributed, 433
  capillaries of, 424
  development of, 812
  function of, 437. *See* Urine.
  Malpighian corpuscles of, 429
  nerves, 435
  tubules of, 429
Knee, pain of, in diseased hip, 559
Krause's membrane, 480
Kreatinin, 447
Kymograph, 186
  tracings, 186, *et seq.*
  spring-, 187

L.

Labia externa and interna, 742
Labyrinth of the ear, 674 *et seq.*
  membranous, 678
  osseous, 674
  function of, 685
Lachrymal apparatus, 691
  gland, *ib.*
Lactation, 406
Lacteals, 362
  absorption by, 375
  contain lymph in fasting, 373
  origin of, 363
  structure of, 364
  in villi, 324
Lactic acid, 857
  in gastric fluid, 304
Lactiferous ducts, 406
Lactose, 266, 409
Lacunæ of bone, 53
Lamellæ of bone, 55
Lamina spiralis, 676
  use of, 686
Laminæ dorsales, 762
  viscerales or ventrales, 767
Language, how produced, 530
Large intestine, 325. *See* Intestine.
Larynx, construction of, 520
  muscles of, 521
  nerves of, 522
  variations in according to sex and age, 527
  ventricles of, 530
  vocal cords of, 520
Latent period, 497
Laughing, 248
Laxator tympani muscle, 685
Lead an accidental element, 860
Leaping, 54
Lecithin, 341
Legumen identical with casein, 267
Lens, crystalline, 700
Lenticular ganglion, relation of third nerve to, 625
Leucic acid, 857
Leucin, 330
Leucocytes,
  of blood, 98
  amœboid movements, 99
  chyle, 374
  lymph, 372
  origin of, 122
Leucocythæmia, state of vascular glands in, 464
Levers, different kinds of, 507
Lieberkühn's glands,
  in large intestines, 326
  in small intestines, 317
Life, 837
  relation to other forces, 818
  simplest manifestations of, 8
Ligamentum nuchæ, 39
Lightning, condition of blood after death by, 89
Lime, salts of, in human body, 859
Lingual branch of fifth nerve, 285
Lips, influence of fifth nerve on movements of, 624
Liquor amnii, 770
Liquor sanguinis, or plasma, 78
  lymph derived from, 376
  still layer in capillaries, 197
Lithium, absorption of salts of,
Liver, 332
  action of, on albuminous matters, 348
    on saccharine matters, 349
  blood-elaborating organ, 347
  blood-making organ, 120
  blood-vessels of, 336
  capillaries of, *ib.*
  cells of, 333
  circulation in, 334
  development of, 809

Liver, *continued.*
  ducts of, 336
  functions of, 338
    in fœtus, 344
  glycogenic function of, 348
  secretion of, 338. *See* Bile.
  structure of, 333
  sugar formed by, 350 *et seq.*
Locus niger, 591
Loss of water, 858
Ludwig's air pump, 110
Lungs, 221
  blood-supply, 226
  capillaries of, 166
  cells of, 223
  changes of air in, 238
  changes of blood in, 244
  circulation in, 226
  contraction of, 237
  coverings of, 222
  development of, 810
  elasticity of, 231
  lobes of, 223
  lobules of, 223
  lymphatics, 226
  muscular tissue of, 237
  nerves, 227
  nutrition of, 226
  position of, 215
  structure of, 222
Luxus consumption, 274
Lymph, 373
  compared with chyle, 373
    with blood, 374
  current of, 368
  quantity formed, 375
  source of, 376
Lymph-corpuscles, 373
  in blood, 122
  development of into red blood-corpuscles, *ib.*
  origin of, *ib.*
Lymph-hearts, structure and action of, 377
  relation of to spinal cord, 377
Lymphatic glands, 368
Lymphatic vessels, 361
  absorption by, 376
  communication with serous cavities, 365
  communication with blood-vessels, *ib.*
  contraction of, 368
  course of fluid in, 368
  distribution of, 361
  origin of, 363
  propulsion of lymph by, 368
  structure of, 368 *et seq.*
  valves of, 368
Lymphoid or retiform tissue, 40. *See* Adenoid Tissue.

M.

Macula germinativa, 740
Magnesium, 859
Male sexual functions, 750
Malleus, 673
  function of, 682
Malpighian bodies or corpuscles of kidney, 429
  capsules, *ib.*
  corpuscles of spleen, 464
Maltose, 285, 853
Mammalia,
  blood-corpuscles of, 96
  brain of, 606
Mammary glands, 405
  evolution, 407
  involution, 407
  lactation, 406
Mandibular arch, 783
Manganese, 860
Manometer, 186
  experiments on respiratory power with, 238
Marrow of bone, 52
Mastication, 278
  fifth nerve supplies muscles of, 278
  muscles of, 278
Mastoid cells, 673
Matrix of cartilage, 46
  of nails, 421
Mature corpuscles,
  origin of, 120
Meatus of ear, 672
  urinarius, opening of in female, 742
Meckel's cartilage, 783
Meconium, 344
Medulla of bone, 52
  of hair, 420
Medulla oblongata, 583 *et seq.*
  columns of, 583
  conduction of impressions, 587
  decussation of fibres, 584
  development, 801
  effects of injury and disease of, 588
  fibres of, how distributed, 585
  functions of, 587 *et seq.*
  important to life, 588
  nerve-centres in, 588
  pyramids of, anterior, 584
    posterior, 585
  structure of, 584
Medullary portion of kidney, 429
  substance of lymphatic glands, 369
  substance of nerve fibre, 543
Melanin, 852
Membrana decidua, 745
  granulosa, 739
    development of into corpus luteum, 747
  limitans externa, 697
    interna, 695

- Membrana propria or basement membrane, 397. *See* Basement Membrane.
  - pupillaris, 805
    - capsulo-pupillaris, *ib.*
  - tympani, 673
    - office of, 680
- Membrane, blastodermic, 760
  - Jacob's, 697
  - of the brain and spinal cord, 564
  - ossification in, 57
  - primary or basement, 394. *See* Basement membrane.
  - vitelline, 739
- Membranes, mucous, 396. *See* Mucous membranes.
- Membranes, passage of fluids through, 366
  - secreting, 398
- Membranes, serous, 394. *See* Serous membranes.
- Membranous labyrinth, 678
- Memory, relation to cerebral hemispheres, 608 *et seq.*
- Menstrual discharge, composition of, 745
- Menstruation, 744
  - coincident with discharge of ova, 744
  - corpus luteum of, 747
  - time of appearance and cessation, 747
- Mental derangement, 609
  - exertion, effect on heat of body, 391
    - on phosphates in urine, 448
  - faculties, development of in proportion to brain, 609
    - theory of special localisation of, 610 *et seq.*
  - field of vision, 719
- Mercurial air-pump, 110
- Mercurial manometer, 185
- Mercury, absorption of, 426
- Mesencephalon, 801
- Mesoblast, 760
- Mesocephalon, 590
- Metalbumin, 845
- Metallic substances, absorption of by skin, 426
- Metencephalon, 801
- Methæmoglobin, 115
- Mezzo-soprano voice, 426
- Micturition, 460
- Milk, as food, 307
  - chemical composition, 409
  - properties of, 409
  - secretion of, 406
- Milk-curdling ferments, 331, 410
- Milk-globules, 409
- Milk-teeth, 77 *et seq.*
- Millon's re-agent, 845
- Mind, cerebral hemisphere the organs of, 608
  - influence on action of heart, 154
- Mind, *continued.*
  - influence on animal heat, 391
    - on digestion, 360
    - on hearing, 689
    - on movements of intestines, 360
    - on secretion, 404
    - on secretion of saliva, 286
    - in vision, 719 *et seq.*
  - power of concentration on the senses, 723
    - of exciting sensations, 649
- Mitral valve, 133
- Modiolus, 675
- Molecules, or granules, 8
  - in blood, 94
  - in milk, 409
  - movement of in cells, 8
- Molars, 75
- Molecular base of chyle, 373
  - motion, 8
- Monamides, 848
- Motion, causes and phenomena of, 474
  - amœboid, 8, 99, 475
  - ciliary, 7, 474
  - molecular, 8
  - muscular, 488 *et seq.*
  - of objects, how judged, 722
  - power of, not essentially distinctive of animals, 4
  - sensation of, 650
- Motor impulses, transmission of in cord, 576
  - nerve-fibres, 554
    - laws of action of, 557
- Motor linguæ nerve, 635
  - oculi, or third nerve, 620
- Motorial end-plates, 549
- Mouth, changes of food in, 276 *et seq.*
- Movements,
  - of eyes, 728
  - of intestines, 359
  - of voluntary muscles, 507
  - produced by irritation of auditory nerve, 690
- Mucigen, 290
- Mucin, 290
- Mucous membrane, 396
  - basement membrane of, 397
  - capillaries of, 167
  - epithelium-cells of, 398. *See* Epithelium.
  - digestive tract, 396
  - gastro-pulmonary tract, 397
  - genito-urinary tract, 397
  - gland-cells of, 397
  - of intestines, 315, 325
  - of stomach, 298
  - of tongue, 661
  - of uterus, changes of in pregnancy, 773
  - respiratory tract, 397
- Muco-salivary glands, 282
- Mucus, 398

Mucus, *continued.*
  in bile, 341
  in urine, 446
  of mouth, mixed with saliva, 283
Müller's fibres, 698
Murexide, 445, 851
Muscles,
  activity, 488
  changes in, by exercise, 500
  chemical constitution, 485, 502
  clot, 485
  contractility, 488
  contraction, mode of, 494
  corpuscles, 481
  curves, 497 *et seq.*; 502
  development, 483
  disc of Hensen, 480
  effect of pressure of, on veins, 202
  elasticity, 484
  electric currents in, 485, 502
  fatigue, 499
    curves, *ib.*
  growth, 484
  heart, 482
  heat developed in contraction of, 500
  involuntary, 476
    actions of, 503, 511
  Krause's membrane, 480
  muscle-rods, 482
  natural currents, 485
  nerves of, 483
  non-striated, 476
  nutrition of, 483
  physiology of, 484
  plain, 476
  plasma, 485
  reaction, 485
  response to stimuli, 503
  rest of, 484
  rigor, 504
  sarcolemma, 478
  sensibility of, 489
  serum, 485
  shape, changes in, 501
  sound developed in contraction of, 501
  source of action of, 512
  stimuli, 489
  striated, 478
  structure, 478 *et seq.*
  tetanus, 498
  unstriped, 476
  voluntary, 478
    actions of, 507
    blood-vessels and nerves of, 483
  work of, 499
Muscular action, 503
  conditions of, 502
  force, 499
  source, 512
Muscular irritability, 503
    duration of, after death, 504
Muscular motion, 476
  sense, 653
    cerebellum the organ of, 599
  tone, 582
Muscularis mucosæ, 293, 298, 316
Musculi papillares, 135
Musculo-cutaneous plate, 780
Musical sounds, 688
Myograph, 495
  pendulum, 495
Myopia, or short-sight, 708
Myosin, 485

N.

Nabothi glandulæ, 742
Nails, 421
  growth of, 421
  structure of, 421
Naphthilamine, 330
Nasal cavities in relation to smell, 668 *et seq.*
Native albumins, 845
Natural organic compounds, 844
  classification of, *ib.*
Nerve-centre, 548. *See* Cerebellum, Cerebrum, &c.
  ano-spinal, 581
  automatic action, 563
  cardio-inhibitory, 157, 589
  cilio-spinal, 587
  conduction in, 558
  deglutition, 296, 589
  diabetic, 590
  diffusion in, 559
  functions of, 558
  genito-urinary, 581
  mastication, 279, 589
  radiation in, 559
  reflexion in, *ib.*
    laws and conditions of, 560
  respiratory, 250, 588
  secretion of saliva, 286, 589
  transference of impressions, 558
  vaso-motor, 191, 589
  vesico-spinal, 581
Nerve-corpuscles,
  caudate or stellate, 549
  polar, 550
Nerves, 540
  accelerator, 158
  action of stimuli on, 514
    currents of, 513
  afferent, 554
  axis-cylinder of, 542
  centrifugal, 554
  centripetal, 554
  cerebro-spinal, 540
  classification, 542, 554

- Nerves, *continued.*
  - conduction by, 553 *et seq.*
    - rate of, 554
  - continuity, 545
  - course of, 545
  - cranial, 619. *See* Cerebral Nerves.
  - depressor, 192
  - efferent, 554
  - electrical currents of, 513
  - functions of, 552
    - effect of chemical stimuli on, 514
      - of mechanical irritation, 514
      - of temperature, 514
  - funiculi of, 541
  - grey, 544
  - impressions on, referred to periphery 555
  - inhibitory, 554. *See* Inhibitory Action.
  - intercentral, 554
  - laws of conduction, 555
    - of motor nerves, 557
    - of sensory nerves, 555
  - medullary sheath, 542
  - medullated, 542
  - motor, 554
    - laws of action in, 557
  - natural currents, 513
  - neurilemma, 541
  - nodes of Ranvier, 543
  - non-medullated, 544
  - nuclei, 542
  - of special sense, 557
  - plexuses of, 546
  - primitive nerve sheath, 542
  - sensory, 554
    - laws of action in, 555
  - size of, 544
  - spinal, 569, 572, 636 *et seq.* *See* Spinal Nerves.
  - stimuli, 514
  - structure, 541
  - sympathetic, 540, 636. *See* Sympathetic Nerve.
  - terminations of, 549
    - central, 550
    - in cells, 549
    - in end-bulbs, 548
    - in motorial end-plates, 549
    - in networks or plexuses, 549
    - in Pacinian corpuscles, 547
    - in touch-corpuscles, 548
  - trophic, 625, 645
  - ulnar, effect of compression of, 555
  - varieties of, 541
  - vaso-constrictor, 194
  - vaso-dilator, *ib.*
  - vaso-inhibitory, *ib.*
  - vaso-motor, *ib.*
  - white, 514
- Nervi nervorum, 556
- Nervi vasorum, 164
- Nervous force, velocity of, 554
- Nervous system, 540
  - cerebro-spinal, 540
  - development, 798
  - elementary structure of, 540
  - influence of
    - on animal heat, 391
    - on arteries, 192 *et seq.*
    - on contractility, 488
    - on contraction of blood-vessels, 190
    - on erection, 211
    - on gastric digestion, 312
    - on the heart's action, 154
    - on movements of intestines, 359
      - of stomach, 312
    - on nutrition, 645
    - on respiration, 249
    - on secretion, 285
    - on sphincter ani, 357
  - sympathetic, 636
- Network, intracellular, 11
  - nuclear, 13
- Neurilemma, 541
- Neurin, 849
- Neuroglia, 41
- Nipple, an erectile organ, 210
  - structure of, 406
- Nitrogen,
  - in blood, 118
  - influence of in decomposition, 844
  - in relation to food, 263 *et seq.*
  - in respiration, 241
- Nitrogenous compounds, 264
  - non-nitrogenous compounds, 264
- Nitrogenous equilibrium, 538
- Nitrogenous food, 265
  - in relation to muscular work, 456 *et seq.*
  - in relation to urea, *ib.*
    - to uric acid, 458
- Nodes of Ranvier, 543
- Noises in ears, 557
- Non-azotized or Non-nitrogenous food 264
  - organic principles, 852
- Nose, 666. *See* Smell.
  - irritation referred to, 559
- Notochord, 764
- Nucleus, 11
  - position, 12
  - staining of, 12
- Nutrition, 533
  - general nature,
    - of nervous system, 641
    - of trophic nerves, 645
  - in paralysed parts, 644
  - of cells, 10
- Nymphæ, 742

O.

- Ocular cleft, 804
  - spectrum, 725 *et seq.*
- Odontoblasts, 73
- Odours,
  - causes of, 669 *et seq.*
  - different kinds of, 670
  - perception of, *ib.*
    - varies in different classes, *ib.*
  - relation to taste, 665
- Œsophagus, 292
- Oil, absorption of, 375
- Oleaginous principles, digestion of, 331
- Oleic acid, 856
- Olfactory cells, 668
  - nerve, 667
    - subjective sensations of, 671
- Olivary body, 584
  - fasciculus, 584
- Omphalo-mesenteric,
  - arteries, 791
  - duct, 778
  - veins, 791
- Oncograph, 452
- Oncometer, *ib.*
- Ophthalmic ganglion, relation of third nerve, 620
- Ophthalmoscope, 716
- Optic,
  - lobes, corpora quadrigemina homologues of, 592
    - functions of, 593
  - nerve, decussation of, 732
    - point of entrance insensible to light, 713
  - thalamus, function of, 594
  - vesicle, primary, 802
    - secondary, 803
- Optical angle, 720
  - apparatus of eye, 699
- Ora serrata of retina, 695
- Orang,
  - brain of, 608
- Organ of Corti, 676
- Organic compounds in body, 843
  - instability of, 844
- Organs, plurality of cerebral, 611
- Organs of sense, development of, 802
- Osmosis, 378
- Os orbiculare, 673
- Os uteri, 742
- Osseous labyrinth, 674
- Ossicles of the ear, 673
  - office of, 682
- Ossicula auditus, 673
- Ossification, 57 *et seq.*
- Osteoblasts, 58
- Osteoclasts, 63
- Otoconia or Otoliths, 678
  - use of, 685
- Ovaries, 737
- Ovaries, *continued.*
  - enlargement of, at puberty, 741
  - Graafian vesicles in, 738
- Ovisacs, 738
- Ovum, 739
  - action of seminal fluid on, 758
  - changes of, in ovary, 740
      - previous to formation of embryo, 758
      - subsequent to cleavage, 761 *et seq.*
    - in uterus, 759 *et seq.*
  - cleaving of yelk, 758
  - connexion of with uterus, 737
  - discharge of from ovary, 743
  - formation of, 740
  - germinal membrane of, 760
  - germinal vesicle and spot of, 740
  - impregnation of, 758
  - structure of, 739
  - unimpregnated, 739
- Oviduct, or Fallopian tube, 741
- Oxalic acid, 449
- Oxalic acid in urine, 449
- Oxygen, 843
  - in blood, 110
  - consumed in breathing, 241
  - effects of on colour of blood, 108
  - proportion of to carbonic acid, 238 *et seq.*
- Oxyhæmoglobin, 112
  - spectrum, 114

P.

- Pacinian bodies or corpuscles, 547
- Palate and uvula in relation to voice, 529
  - cleft, 783
- Palmitin, 855
- Pancreas, 328
  - development of, 808
  - functions of, 328
  - structure, 328
- Pancreatic fluid, 329
- Pancreatin, 854
- Papilla foliata, 664
- Papillæ
  - of the kidney, 428
  - of skin, distribution of, 413
    - end-bulbs in, 416
  - epithelium of, 414
    - nerve-fibres in, 415
    - supply of blood to, 414
    - touch corpuscles in, 415
  - of teeth, 73
  - of tongue, 661 *et seq.*
    - circumvallate or calyciform, 661
    - conical or filiform, 662
    - fungiform, *ib.*
- Paraglobulin, 86 *et seq.*
- Paralbumin, 845

Par vagum, 631. *See* Pneumogastric nerve.
Paralysed parts,
    nutrition of, 644
    pain in, 556
  limbs, temperature of, 391
  preservation of sensibility in, 576
Paralysis, cross, 576
Parapeptone, 306
Paraplegia,
  delivery in, 581
  reflex movements in, *ib.*
  state of intestines in, 360
Parotid gland, saliva from, 279, 289
  nerves influencing secretion by, 289
Pause in heart's action, 144
  respiratory, 233
Pecten of birds, 804
Peduncles,
  of the cerebellum, 598
  of the cerebrum, or Crura Cerebri, 590
Pelvis of the kidney, 428
Penis,
  corpus cavernosum of, 210
  development of, 818
  erection of, explained, 210
  reflex action in, 581
Pepsin, 301
Pepsinogen, 301
Peptic cells, 299
Peptones, 305 *et seq.*
Perceptions of sensations by cerebral hemispheres, 609
Pericardium, 127
Perichondrium, 59
Perilymph, or fluid of labyrinth of ear, 674
  use of, 685
Perimysium, 478
Perineurium, 541
Periosteum, 52
Peristaltic movements of intestines, 359
  of stomach, 308
Perivascular lymphatic sheaths, 172
Permanent teeth, 76. *See* Teeth.
Perspiration, cutaneous, 424
  insensible and sensible, 424
  ordinary constituents of, 424
Peyer's glands, 318
  patches, 318
  resemblance to vascular glands, 461
  structure of, 318
Pflüger's law, 517
Phakoscope, 704
Pharynx, 291
  action of in swallowing, 295
  influence of glosso-pharyngeal nerve on, 296
    of pneumogastric nerve on, 296
Phenol, 857
Phosphates, 859
Phosphates in tissues, 859
Phosphorus in the human body, *ib.*
Pia mater, circulation in, 208
Pigment, 24
  of hair, 418
  of retina, 697
  of skin, 412
Pigment cells, forms of, 24
  movements of granules in, 24
Pineal gland, 472
Pinna of ear, 672
Pituitary body, 472
  development, 781
Placenta, 773 *et seq.*
  fœtal and maternal, *ib.*
Plants,
  distinctions from animals, 3. *See* also Vegetables.
Plasma of blood, 80
  salts of, 105
Plasmine, 84
  composition, 85
  nature of, 84
Plethysmograph, 191
Pleura, 221
Plexus, terminal, 549
  of spinal nerves, relation to cord, 546
  myentericus, 315
  Auerbach's, 315
  Meissner's, 316
Pneumogastric nerve, 631
  distribution of, *ib.*
  influence on
    action of heart, 156
    deglutition, 295
    gastric digestion, 312
    larynx, 296
    lungs, 250
    œsophagus, 633
    pharynx, 633
    respiration, 250
    secretion of gastric fluid, 312
    sensation of hunger, 270
    stomach, 312
  mixed function of, 631
  origin from medulla oblongata, 586
Poisoned wounds, absorption from, 381
Pons Varolii, its structure, 590
  functions, *ib.*
Portal,
  blood, characters of, 108
  canals, 336
  circulation, 334
    function of spleen with regard to, 465
  veins, arrangement of, 336 *et seq.*
Portio dura, of seventh nerve, 628
  mollis, of seventh nerve, 678
Post mortem digestion, 313
Potassium, 859
  sulphocyanate, 283
Pregnancy, absence of menstruation during, 747

Pregnancy, *continued*.
  corpus luteum of, 750
  influence on blood, 107
Presbyopia, or long-sight, 712
Primitive groove, 762
Primitive nerve-sheath, or Schwann's sheath, 543
Processus gracilis, 673
Propionic acid, 856
Prosencephalon, 801
Prostate gland, 750
Proteids, 305
  chemical properties, 845 *et seq.*
  physical properties, *ib.*
  tests for, 845
  varieties of, *ib.*
Proteolytic ferments, 307
Protoplasm, 6
  chemical characters, *ib.*
  movement, *ib.*
  nutrition, 10
  physical characters, 6
  physiological characters, *ib.*
  reproduction, 13
  transformation of, 17
Proto-vertebræ, 764
Pseudoscope, 735
Ptyalin, 283
  action of, 285
Puberty,
  changes at period of, 746
  indicated by menstruation, *ib.*
Pulmonary artery, valves of, 136
  capillaries, 166
  circulation, 226
Pulse, arterial, 177
  cause of, *ib.*
  dicrotous, 182
  difference of time in different parts, 178
  frequency of, 151
  influence of age on, *ib.*
    of food, posture, etc., 152
  relation of to respiration, 152
  sphygmographic tracings, 180 *et seq.*
  variations, 181 *et seq.*
  in capillaries, 198
Purkinje's figures, 714
Pylorus, structure of, 299
  action of, 309
Pyramidal portion of kidney, 428
Pyramids of medulla oblongata, 584

Q.

Quadrupeds, retinæ of, 732
Quantity of air breathed, 234
  blood, 79
  saliva, 283

R.

Racemose glands, 399
Radiation of impressions, 559
Rectum, 325
Recurrent sensibility, 573
Reflex actions, 559
  acquired, 562
  augmentation, 563
  classification, 561
  compound, 562
  conditions necessary to, 560
  in disease, 580
  examples of, 563
  excito-motor and sensori-motor, 560
  inhibition of, 563, 578
  irregular in disease, 580
    after separation of cord from brain, 577
  laws of, 460
  morbid, 580
  of medulla oblongata, 587 *et seq.*
  of spinal cord, 577
  purposive in health, 560
  relation between a stimulus and, 561
  secondary, 562
  simple, 562
Refracting media of eye, 700
Refraction, laws of, *ib.*
Regions of body. *See* Frontispiece.
Registering apparatus,
  cardiograph, 148
  kymograph, 186
  sphygmograph, 178
Relations between secretions, 404
Reptiles,
  blood-corpuscles, 95
  brain, 606
Reserve air, 234
Residual air, 234
Respiration, 214
  abdominal type, 231
  changes of air, 240
    of blood, 244
  costal type, 231
  force, 236
  frequency, *ib.*
  influence of nervous system, 249
  mechanism, 228 *et seq.*
  movements, 228. *See* Respiratory Movements.
  nitrogen in relation to, 241
  organic matter excreted, 242
  quantity of air changed, 235
  relation to the pulse, 152, 263
  suspension and arrest, 258
  types of, 231
Respiratory capacity of chest, 235
  cells, 224
  functions of skin, 426
  movements, 228
    axes of rotation, 228 *et seq.*
    of air tubes, 218

Respiratory movements, *continued.*
  of glottis, 234
  influence on amount of carbonic acid, 239
    on arterial tension, 263
  rate, 236
    relation to pulse rate, 236
      size of animal, *ib.*
  relation to will, 249
  various mechanism, 245
 muscles, 228 *et seq.*
  daily work, 235
  power of, 237
 nerve-centre, 249
 rhythm, 233
 sounds, 233
Restiform bodies, 585
Rete mucosum, 412
 testis, 751
Retiform or adenoid, or lymphoid tissue, 40
Retina, 694
 blind spot, 713
 blood-vessels, 699
 duration of impressions on, 714
  of after-sensations, 715
 effect of pressure on, 730
 excitation of, 713
 focal distance of, 703
 fovea centralis, 695, 713
 functions of, 713
 image on, how formed distinctly, 699
  inversion of, how corrected, 717
 insensible at entrance of optic nerve, 713
 layers, 695
 in quadrupeds, 732
 reciprocal action of parts of, 726
 in relation to direction of vision, 721
  to motion of bodies, 722
  to single vision, 729
  to size of field of vision, 719
 reflection of light from, 716
 structure of, 694
 vessels, 699
 visual purple, 716
Rheoscopic frog, 515
Rhinencephalon, 801
Ribs, axis of rotation, 228 *et seq.*
Rigor mortis, 504
 affects all classes of muscles, *ib.*
 phenomena and causes of, 505
Rima glottidis, movements of in respiration, 234
Ritter's tetanus, 518
Rods of Corti, 677
 use of, 687
Rouleaux, formation of in blood, 94
Ruminants,
 stomach of, 296
Rumination, *ib.*
Running, mechanism of, 511

Rut or heat, 743

S.

Saccharine principles of food, digestion of, 352
Sacculus, 678
Saliva, 282
 composition, 283
 process of secretion, 285
 quantity, 283
 rate of secretion, *ib.*
 uses, 284
Salivary glands, 279
 development of, 808
 influence of nervous system, 285
 mixed, 283
 nerves, 282
 secretion, 282
 structure, 279
 true, 281
 varieties, 280
Sarcode, 6. *See* Protoplasm.
Sarcolemma, 478
Sarcosin, 849
Sarcous elements, 479
Scala media, 676
 tympani, *ib.*
 vestibuli, *ib.*
Sclerotic, 692
 blood-vessels, 699
Scurvy from want of vegetables, 268
Sebaceous glands, 417
 their secretion, 423
Sebacic acid, 857
Secreting glands, 398
 aggregated, 399
 convoluted tubular, *ib.*
 tubular or simple, *ib.*
Secreting membranes, 394. *See* Mucous and Serous membranes.
Secretion, 393
 apparatus necessary for, 393 *et seq.*
 changes in gland-cells during, 402
  ,, ,, pancreas, 329
  ,, ,, stomach, 301
  ,, ,, salivary glands, 289
 circumstances influencing, 403
 discharge of, 402
 general nature of, 393
 influence of nervous system, 404
 process of physical and chemical, 401, 402
 serous, 395
 synovial, 396
Segmentation of cells, 757
 ovum, 757
Semen, 756
 composition of, *ib.*
 emission of, a reflex act, 581
 filaments or spermatozoa, 752
  purpose of, 756
 tubes, 752

SEMICIRCULAR.

Semicircular canals of ear, 675
  development of, 805 *et seq.*
  use of, 685
Semilunar valves, 136
  functions of, 141
Semilunes of Heidenhain, 281
Sensation, 646
  colour, 723
  common, 646
  conditions necessary to, 648
  excited by mind, 648
    by internal causes, *ib.*
  of motion, 650
  nerves of, 619 *et seq.*
    impressions on referred to periphery, 553
    laws of action, 553
  objective, 648
  of pain, 651
  of pressure, 655
  special, 647
    nerves of, 619
  stimuli of, 557
    of special, 557
  subjective, 557, 658. *See* also Special Senses, 648.
  tactile, 651
  temperature, 656
  tickling, 652
  touch, 651
  transference and radiation of, 558 *et seq.*
  of weight, 655
Sense, special, 646
  of hearing, 671. *See* Hearing, Sound.
  of sight, 691. *See* Vision.
  of smell, 666. *See* Smell.
  of taste, 658. *See* Taste.
  of touch, 651. *See* Touch.
  muscular, 655
  organs of, development of, 802
Sensory impressions, conduction of, 555
    by spinal cord, 573
  nerves, 554
Septum between auricles, formation of, 789
  between ventricles, formation of, *ib.*
Serous fluid, 395
Serous membranes, 394
  arrangement of, *ib.*
  communication of lymphatics with, 366
  epithelium, 394
  fluid secreted by, 395
  functions, *ib.*
  lining joints, etc., *ib.*
    visceral cavities, *ib.*
  stomata, 366
  structure of, 394
Serum,
  of blood, 115

SOBBING.

Serum, *continued.*
  separation of, 81, 115
Seventh cerebral nerve, auditory portion, 678
  facial portion, 628
Sex, influence on blood, 108
  influence on production of carbonic acid, 239
  relation of to respiratory movements, 231
Sexual organs and functions in the female, 736
  in the male, 750
Sexual passion, connection of with cerebellum, 599
Sighing, mechanism of, 246
Sight, 691. *See* Vision.
Silica, parts in which found, 859
Silicon, *ib.*
Singing, mechanism of, 248, 526 *et seq.*
Single vision, conditions of, 729
Sinus pocularis, 817
  urogenitalis, *ib.*
Sinuses of dura mater, 208
Sixth cerebral nerve, 627
Size of field of vision, 719
Skeleton. *See* Frontispiece.
Skin, 410
  absorption by, 426
    of metallic substances, *ib.*
    of water, *ib.*
  cutis vera of, 413
  epidermis of, 411
  evaporation from, 387
  excretion by, 424
  exhalation of carbonic acid from, 424
    of watery vapour from, 424
  functions of, 422
    respiratory, 425
  papillæ of, 413
  perspiration of, 424
  rete mucosum of, 412
  sebaceous glands of, 417
  structure of, 410
  sudoriparous glands of, 416
Sleep, 617
Smell, sense of, 666
  conditions of, *ib.*
  delicacy, 669
  different kinds of odours, 670
  impaired by lesion of facial nerve, 629
  impaired by lesion of fifth nerve, 625
  internal excitants of, 671
  limited to olfactory region, 667
  relation to common sensibility, 669
  structure of organ of, 667
  subjective sensations, 671
  varies in different animals, 670
Sneezing, caused by sun's light, 559
  mechanism of, 248
Sniffing, mechanism of, 248
  smell, aided by, 667
Sobbing, 248

Sodium, 859
  in human body, *ib.*
  salts of in blood, 106
Solitary glands, 319
Soluble ferments, 852
Somatopleure, 765
Somnambulism, 563
Sonorous vibrations, how communicated in ear, 679 *et seq.*
  in air and in water, *ib.* *See* Sound.
Soprano voice, 526
Sound,
  binaural sensations, 690
  conduction of by ear, 679
    by external ear, 679
    by internal ear, 685
    by middle ear, 680
  movements and sensations produced by, 691
  perception,
    of direction of, 688
    of distance of, 689
  permanence of sensation of, 689
  produced by contraction of muscle, 501
  production of, 688
  subjective, 690
Source of water, 858
Spasms, reflex acts, 580
Speaking, 530
  mechanism of, 248, 530
Special senses, 647
Spectrum-analysis of blood, 114
Spectrum or ocular after-sensation, 725
Speech, 530
  function of tongue in, 533
  influence of medulla oblongata on, 589
Spermatozoa, development of, 752
  form and structure of, 753
  function of, 756
  motion of, 756
Spherical aberration, 710
  correction of, *ib.*
Spheroidal epithelium, 27
Sphincter ani, 325, 357
  external, 357
  internal, 325
  influence of spinal cord on, 357
Sphygmograph, 178
  tracings, 180 *et seq.*
Spinal accessory nerve, 635
Spinal cord, 565
  automatism, 583
  canal of, 566
  centres in, 580
  a collection of nervous centres, 580
  columns of, 566
  commissures of, *ib.*
  conduction of impressions by, 573 *et seq.*
  course of fibres in, 571
  decussation of sensory impressions in, 575
Spinal cord, *continued.*
  effect of injuries of, on conduction of impressions, 575 *et seq.*
    on nutrition, 645
  fissures and furrows of, 566
  functions of, 574
    of columns, 575
  influence on lymph-hearts, 581
    on sphincter ani, *ib.*
    on tone, 582
  morbid irritability of, 580
  nerves of, 569
  reflex action of, 577
    in disease, 580
    inhibition of, 578
  size of different parts, 567
  special centres in, 580
  structure of, 565 *et seq.*
  transference, 577
  weight, 607
    relative, *ib.*
  white matter, 567
    grey matter, 568
Spinal nerves, 569, 636
  origin of, 569
  physiology of, 572
Spiral canal of cochlea, 671
  lamina of cochlea, *ib.*
    function of, 682
Spirometer, 235
Splanchnic nerve, 192, 312
Splanchnopleure, 765
Spleen, 461
  functions, 464
  hilus of, 461
  influence of nervous system, 466
  Malpighian corpuscles of, 464
  pulp, 463
  stroma of, *ib.*
  structure of, *ib.*
  trabeculæ of, *ib.*
Splenic vein, blood of, 109
Spot, germinal, 740
Squamous epithelium, 23
Stammering, 533
Stapedius muscle, 674
  function of, 685
Stapes, 673
Starch, 285
  digestion of
    in small intestine, 331, 354
    in mouth, 285
    in stomach, 307, 354
Starvation, 270
  appearances after death, 272
  effect on temperature, 271
  loss of weight in, *ib.*
  period of death in, *ib.*
  symptoms, *ib.*
Steapsin, 331
Stearic acid, 856
Stearin, 855
Stercorin, 345

Stercorin, *continued.*
  allied to cholesterin, 345
Stereoscope, 722
St. Martin, Alexis, case of, 303
Stomach, 296
  blood-vessels, 302
  development, 806, *et seq.*
  digestion in, 303
    circumstances favouring, 307
    products of, 306
  digestion after death, 313
  glands, 299
  lymphatics, 302
  movements, 308
    influence of nervous system, 312
  mucous membrane, 298
  muscular coat, 298
  nerves, 307
  ruminant, 296
  secretion of, 303. *See* Gastric fluid.
  structure, 297
  temperature, 303
Stomata, 200, 366
Stratum intermedium (Hannover), 74
Striated muscle, 478
Stromühr, 204
Structural basis of human body, 5
Stumps, sensations in, 556
Succinic acid, 857
Succus entericus 351
  functions of, 352
Sucking, mechanism of, 248
Sudoriferous glands, 416
  their distribution, 417
  number of, *ib.*
  their secretion, 424
Suffocation, 257, *et seq.*
Sugar, 856
  as food, experiments with, 272
  digestion of, 352, 354
  formation of in liver, 348, 350
Sulphates, 859
  in tissues, 859
  in urine, 447
Sulphuretted hydrogen, 857
Suprarenal capsules, 469
  development of, 814
  disease of, relation to discoloration of skin, 471
Structure, 469
Sun, a source of energy, 824
Swallowing, 294
  nerves engaged, 295
Sweat, 424
Sympathetic nervous system, 636
  character of movements executed through, 641
  conduction of impressions by, 640
  diagrammatic view, 638
  distribution, 636
  divisions of, 540
  fibres, differences of from cerebro-spinal fibres, 544
Sympathetic nervous system, *continued.*
    mixture with cerebro-spinal fibres, 637
  functions, 640
  ganglia of, 640
    action of, 640 *et seq.*
    co-ordination of movements by, 642
    structure, 637
    in substance of organs, 642
  influence on
    animal heat, 391
    blood-vessels, 190 *et seq.*
    heart, 158
    intestines, 359
    involuntary motion, 640 *et seq.*
    salivary glands, 285 *et seq.*
    secretion, *ib.*
    stomach, 312
  structure of, 637
Synovial fluid, secretion of, 396
  membranes, 396
Syntonin, 306, 846
Systemic circulation, 124. *See* Circulation.
  vessels, *ib.*
Systole of heart, 147

T.

Taste, 658
  after-tastes, 666
  conditions for perception of, 658
  connection with smell, 665
  impaired by injury
    of facial nerve, 629
    of fifth nerve, 626
  nerves of, 626, 630
  seat of, 658
  subjective sensations, 666
  varieties, 665
Taste-goblets, 664
Taurin, 849
Taurocholic acid, 339
Teeth, 67
  development, 71
  eruption, times of, 77
  structure of, 68 *et seq.*
  temporary and permanent, 75 *et seq.*
Temperament, influence on blood, 108
Temperature, 382
  average of body, *ib.*
  changes of, effects of, 383 *et seq.*
  circumstances modifying, 386
  of cold-blooded and warm-blooded animals, 384
  in disease, *ib.*
  influence on amount of carbonic acid produced, 240
  loss of, 387
  maintenance of, 386
  of Mammalia, Birds, etc., 384

Temperature, *continued.*
  of paralysed parts, 391
  regulation of, 386
  of respired air, 242
  sensation of variation of, 656. *See* Heat.
Tendons, structure of, 38
  cells of, *ib.*
Tenor voice, 526
Tension, arterial, 185
Tension of gases in lungs, 243
Tensor tympani muscle, 674
  office of, 684
Tesselated epithelium, 22
Testicle, 750
  development, 813
  descent of, 815
  structure of, 750 *et seq.*
Tetanus, 498
Thalamencephalon, 801
Thalami optici, function of, 594
Thermogenic nerves and nerve-centres, 391
Thirst, 270
  allayed by cutaneous absorption, 426
Thoracic duct, 361
  contents, 375
Thymus gland, 466
  function of, 468
  structure, 467
Thyro-arytenoid muscles, 527
Thyroid cartilage, structure and connections of, 520
Thyroid-gland, 468
  function of, 469
  structure, 468
Timbre of voice, 526
Tissue, adipose, 42
  areolar, cellular, or connective, 37
  elastic, 38
  fatty, 42
  fibrous, 38
  gelatinous, 39
  retiform, 40
Tissues,
  connective, 33
  elementary structure of, 33 *et seq.*
  erectile, 210
Tone of blood-vessels, 190
  of muscles, 582
  of voice, 526
Tongue, 659
  action of in deglutition, 294
    in sucking, 248
  action of in speech, 533
  epithelium of, 663
  influence of facial nerve on muscles of, 629
  motor nerve of, 635
  an organ of touch, 664
  papillæ of, 661
  parts most sensitive to taste, 665
  structure of, 659
Tonsils, 291
Tooth, 67. *See* Teeth.
Tooth-ache, radiation of, sensation in, 559
Tooth-pulp, 68
Touch, 651
  after sensation, 658
  conditions for perfection of, 652
  connection of with muscular sense, 655
  co-operation of mind with, 658
  function of cuticle with regard to, 410
    of papillæ of skin with regard to, 410
  hand an organ of, 652
  illusions, 655
  modifications of, 651
  a modification of common sensation, 651
  special organs, 652
  subjective sensations, 658
  the tongue an organ of, 653
  various degrees of in different parts, 653
Touch-corpuscles, 416
Trabeculæ cranii, 781
Trachea, 218
Tradescantia Virginica, movements in cells of, 8
Tragus, 672
Transference of impressions, 558
Traube-Hering's curves, 258
Tricuspid valve, 135
  safety-valve action of, 139
Trigeminal or fifth nerve, 622
  effects of injury of, 623
Trophic nerves, 625
Trypsin, 331
Trypsinogen, 329
Tube, Eustachian, 673
Tubercle of Lower, 129
Tubes, Fallopian, 741. *See* Fallopian Tubes.
  looped, of Henle, 431
Tubular glands, 399
  convoluted, *ib.*
  simple, *ib.*
  of intestines, 317, 325
  of stomach, 299
Tubules, 21
Tubuli seminiferi, 752
  uriniferi, 429 *et seq.*
Tunica albuginea of testicle, 750
Tympanum or middle ear, 673
  development of, 805
  functions of, 680
  membrane of, 673
  structure of, *ib.*
  use of air in, 682
Types of respiration, 231
Tyrosin, 330

U.

- Ulceration of parts attending injuries of nerves, 644
- Ulnar nerve,
  - effects of compression of, 553
- Umbilical arteries, 778
  - contraction of, 177
  - cord, 778
  - vesicle, 760, 767
- Unconscious cerebration, 611
- Unorganised ferments, 852
- Unstriped muscular fibre, 476
  - development, 483
  - distribution, 476
  - structure, 477
- Urachus, 771
- Urate of ammonium, 444
  - of sodium, 444
- Urea, 441
  - apparatus for estimating quantity, 443
  - chemical composition of, 442,
  - identical with cyanate of ammonium, *ib.*
  - properties, 441
  - quantity, 443
  - in relation to muscular exertion, 457
  - sources, 456
- Ureides, 851
- Ureter, 436
- Urethra, development of, 818
- Uric acid, 444
  - condition in which it exists in urine, 444
  - forms in which it is deposited, 445
  - proportionate quantity of, 444
  - source of, 458
  - tests, 445
  - variations in quantity, 444
- Urina sanguinis, potûs, et cibi, 440
- Urinary bladder, 430
  - development, 815
  - nerves, 431
  - regurgitation from prevented, 459
  - structure, 430
- Urinary ferments, 438, 855
- Urine, 437
  - abnormal, 441
  - analysis of, 437
  - chemical composition, *ib.*
  - colouring matter of, 446
  - cystin in, 449
  - decomposition by mucus, 438
  - effect of blood-pressure on, 453
  - expulsion, 460
  - extractives, 447
  - flow of into bladder, 459
  - gases, 450
  - hippuric acid in, 446
  - mucus in, 446
  - oxalic acid in, 449
- Urine, *continued.*
  - physical characters, 437
  - pigments, 446
  - quantity of chief constituents, 439
  - reaction of, 438
    - in different animals, 438
    - made alkaline by diet, 439
  - saline matter, 447
  - secretion, 455
    - effects of posture, etc., on, 459
    - rate of, *ib.*
  - solids, 441
    - variations of, 439
  - specific gravity of, 440
    - variations of, 440
  - urates, 444, 445
  - urea, 441
  - uric acid in, 444
  - variations of specific gravity, 440
    - of water, 439
- Urobilin, 446
- Urochrome, 446
- Uroerythrin, 446
- Uses of blood, 113
- Uterus, 741
  - change of mucous membrane of, 745
  - development of in pregnancy, 745
  - follicular glands of, 742
  - masculinus, 817
  - reflex action of, 581
  - structure, 741
- Utriculus of labyrinth, 678
- Uvula in relation to voice, 529

V.

- Vagina, structure of, 742
- Vagus nerve, 286. *See* Pneumogastric.
- Valerianic acid, 856
- Valve, ileo-cæcal, structure of, 326
  - of Vieussens, 595
- Valves of heart, 135
  - action of, 139, *et seq.*
  - bicuspid or mitral, 135
  - semilunar, 136, 141
  - tricuspid, 135, 136
  - of lymphatic vessels, 368
  - of veins, 170 *et seq.*
- Valvulæ conniventes, 317
- Vas deferens, 751
  - development, 813
- Vasa efferentia of testicle, 751
    - of kidney, 434
  - recta of kidney, 435
    - of testicle, 751
  - vasorum, 162
- Vascular area, 768
- Vascular glands, 461
  - in relation to blood, 472
  - several offices of, 472
- Vascular system, development of, 785
- Vaso-constrictor nerves, 194

Vaso-dilator nerves, 194
Vaso-motor influence on blood-pressure, 192 *et seq.*
Vaso-motor nerves, 191
  effect of section, 191 *et seq.*
  influence upon blood-pressure, 192
Vaso-motor nerve-centres, 191
  reflection by, 191
Vegetables and animals, distinctions between, 3
Veins, 168
  anastomoses of, 201
  blood-pressure in, 202
  circulation in, 201 *et seq.*
    rate of, 206
  cardinal, 793
  collateral circulation in, 201
  cranium, 208
  development, 793
  distribution, 168
  effects of muscular pressure on, 202
    of respiration on, 254
  force of heart's action remaining in, 201
  influence of expiration, 255
    inspiration, 253
  influence of gravitation in, 203
  parietal system of, 793 *et seq.*
  pressure in, 202
  rhythmical action in, 202
  structure of, 168
  systemic, 126
  umbilical, 778
  valves of, 170
  velocity of blood in, 206
  visceral system of, 793 *et seq.*
Velocity of blood in arteries, 204
    in capillaries, 206
    in veins, 206
  of circulation, 203
  of nervous force, 554
Vena portæ, 109, 334
Venæ hepaticæ advehentes, 794
    revehentes, *ib.*
Ventilation, 252
Ventricles of heart, 138
  capacity of, 132
  contraction of, 138
    effect on blood-current in veins, 153
  dilatation of, *ib.*
  force of, *ib.*
  of larynx, office of, 530
Ventriloquism, 532, 689
Vermicular movement of intestines, 359
Vermiform process, 325
Vertebræ, development of, 778
Vesicle, germinal, 740
  Graafian, 738
    bursting of, 743
  umbilical, 760, 767
Vesicula germinativa, 740
Vesiculæ seminales, 754
  functions of, 754
  reflex movements of, 581
  structure, 754
Vestibule of the ear, 674
Vestigial fold of Marshall, 796
Vibrations, conveyance of to auditory nerve, 679 *et seq.*
  perception of, 688
  of vocal cords, 520
Vidian nerve, 628
Villi in chorion, 772
  in placenta, 776
Villi of intestines, 321
  action in digestion, 322
Visceral arches, development of, 782
  connection with cranial nerves, 783
  laminæ or plates, 767
Vision, 691
  angle of, 720
  at different distances, adaptation of eye to, 703 *et seq.*
  contrasted with touch, 721
  corpora quadrigemina, the principal nerve-centres of, 592
  correction of aberration, 710 *et seq.*
    of inversion of image, 717
  defects of, 708 *et seq.*
  distinctness of, how secured, 699 *et seq.*
  double, 730
  duration of sensation in, 714
  estimation of the form of objects, 721
    of their direction, 721
    of their motion, 722
    of their size, 720
  field of, size of, 719
  focal distance of, 703
  impaired by lesion of fifth nerve, 624
  influence of attention on, 723
  modified by different parts of the retina, 726
  purple, 716
  in quadrupeds, 732
  single, with two eyes, 732
Visual direction, 721
Vital or respiratory capacity of chest, 235
Vital capillary force, 200
Vital force, 837
Vitellin, 846
Vitelline duct, 767
  membrane, 739
  spheres, 759
Vitreous humour, 701
Vocal cords, 521
  action of in respiratory actions, 234 *et seq.*
  approximation of, effect on height of note, 525
  elastic tissue in, 39
  longer in males than in females, 526

Vocal cords, *continued.*
  position of, how modified, 525
  vibrations of, cause voice, 520
Voice, 518, 526
  of boys, 527
  compass of, 526
  conditions on which strength depends, 527
Voice, human, produced by vibration of vocal cords, 518, 523
  in eunuchs, 527
  influence of age on, 527
    of arches of palate and uvula, 529
    of epiglottis, 524
    of sex, 526
  influence of ventricles of larynx, 530
    of vocal cords, 525
  in male and female, 526
    cause of different pitch, 526
  modulations of, 526
  natural and falsetto, 528
  peculiar characters of, 526
  varieties of, 527
Vomiting, 310
  action of stomach in, *ib.*
  nerve-actions in, 312
  voluntary and acquired, 311
Vowels and consonants, 530
Vulvo-vaginal or Duverney's glands, 743

W.

Walking, 509
Water, 858
  absorbed by skin, 426
    by stomach, 353
  amount,
    in blood, variations in, 102, 107
    exhaled from lungs, 241
      from skin, 425
  forms large part of human body, 858
  influence of on coagulation of blood, 89
Water, *continued.*
  influence of on decomposition, 844
  in urine, excretion of, 450
    variations in, 439
  loss of from body, 858
    uses, *ib.*
  quantity in various tissues, *ib.*
  source, *ib.*
  vapour of in atmosphere, 238
Wave of blood causing the pulse, 177
  velocity of, 178
White corpuscles, 98. *See* Blood-corpuscles, white; *and* Lymph-corpuscles.
White fibro-cartilage, 49
  fibrous tissue, 38
Willis, circle of, 208
Wolffian bodies, 810 *et seq.*
Work of heart, 153

X.

Xanthin, 447
Xantho-proteic reaction, 845

Y.

Yawning, 248
Yelk, or vitellus, 757
  changes of, in Fallopian tube, 758
  cleaving of, *ib.*
  constriction of, by ventral laminæ, 767
Yelk-sac, 767 *et seq.*
Yellow elastic fibre, 36, 39
  fibro-cartilage, 49
  spot of Sömmering, 698
Young-Helmholtz theory, 724

Z.

Zimmermann, corpuscles of, 467
Zona pellucida, 739

THE END.

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